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FOREWORD

Since the first major Symposium on Echinoderm Biology was held in London in 1966, sponsored by the Royal Zoological Society, at least six subsequent meetings have been organised by echinodermologists. These have been held in Washington D.C., U.S.A. (2), Rovinj, Yugoslavia (1), Sydney, Australia (1), London (1); the last two meetings (Sydney and London), within the same year (1978), and Brussels, Belgium. Also, at least four meetings are known to have been held in U.S.S.R. Such has been the surge of interest in the study of echinoderms over the past decade, that there is now a demand for the organisation of regular, and more frequent, meetings. The international representation at these meetings indicates the enormous involvement and co-operation which now exists between colleagues working in this exciting field, the world over.

It is more than evident that the satisfaction and pleasure expressed by Professor Norman Millott, in his foreword to the first Symposium volume (1967), at the resurgence of interest in Echinoderm Biology has been clearly justified and can continue so to be.

This volume presents twelve of the forty-one contributions offered at the Echinoderm Conference, Sydney, 1978. The papers are representative of the wide coverage of topics dealt with during the Conference, including echinoderm palaeontology, physiology, reproduction, ecology, behaviour and taxonomy.

To the speakers and chairmen, and to all those who attended the Sydney Conference, I convey my thanks. I must also thank my Technical Officer, Ms Jan Marshall, and Dr Susan Oldfield (Queen's Fellow at The Australian Museum, February, 1977-1979) for their unstinting assistance in the organisation of the Conference. Thanks are also due to the Department of State Fisheries (N.S.W.), Taronga Park Zoo, McWilliams Wines Pty, Leo Buring Wines Pty, Qantas Airways Ltd, and Trans-Australia Airlines (T.A.A.). To The Australian Museum Society (TAMS) I extend a special thanks for assistance.

This Conference could not have been held without the tremendous support and encouragement afforded to the organiser by Dr D. J. G. Griffin, Director, The Australian Museum, and the very generous financial support of the Trustees of the Museum, to both of whom I offer my very sincere thanks.

DECEMBER 1979 FRANCIS W. E. ROWE

CONTENTS

1. ETUDES TAPHONOMIQUES DU GISEMENT CONTENANT LA FAUNE DES ECHINIDES (L'EOCENE D'ISTRIE).

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SUMMARY

Bacva Spring, near Pican Village in Istria (in the extreme north-west of Yugoslavia) is noted both for the large number of fossil echinoids and number of species to be found there. They can be collected directly from the stratum in which they occur. Many loose specimens may also be found mixed with scree material.

In this paper an account is given of the lithological composition of the fossil-bearing stratum; position in which the echinoid fauna occurs in the rock, i.e. the position in relation to the bedding plane, interrelation of fossils and their random orientation; range of size of fossils found; degree and kind of damage observed and palaeoecological characteristics of the echinoids and accompanying fauna.

Judging by their ecological characters the genera *Conoclypeus* and *Echinolampas* were found *in situ*. The massive test, the enlarged solid base and the reduced jaw system in *Conoclypeus* suggest a habitat of turbulent water and gravelly substrate.

The representatives of other genera e.g. *Cylaster*, *Linthia* and *Macropneustes* among others, having thinner-walled tests, well-developed labrum and ambulacra occurring in funnel-shaped depressions suggest a habitat of deeper water with a silty-clay substrate.

That these two ecologically different groups of echinoids occur together is accounted for by a secondary concentration of the fauna due to redeposition by sediment flow.

INTRODUCTION

L'une des localités les plus riches en échinides fossiles en Yougoslavie c'est la source Bacva, non loin du village Pićan en Istrie. Cette localité est caracterisée non seulement par un grand nombre d'espèces, mais aussi par un très grand nombre d'individus. C'est aussi une des localités rares chez nous où les échinides sont ramassés directement du gisement (dans les plupart des cas on les trouvait naturellement preparés dans les éboulis).

La concentration riche de la faune des échinides dans le gisement a permis l'étude minutieuse a) de la position de la faune en relation à la couche; b) du nombre d'exemplaires sur l'unité de la surface; c) de la relation réciproque de la faune es échinides et de la faune accompagnantes; d) des types d'endommagements des squelettes produits au cours de la fossilisation.

Tout cela nous a permis de former certaines conclusions relatives à la position du gisement fosilifère par rapport aux gisements voisins, ainsi qu'à la manière de sa formation.

REPRESENTATION DU GISEMENT FOSSILIFERE

Dans la region de Pićan (Istrie centrale) les sediments de l'Eocène sont développés sur un grand espace dans le facies calcaire et facies du flysche. Le gisement fossilifère qui est le sujet de cet exposé, se trouve dans le cadre de la série de flysche tout près de la source Bacva à 3 km NW du village de Pićan. Examinant due côte de la source vers la route principale Pićan-Gračište, on peut remarquer le profil suivant: directement au-dessus de la source on a découvert la couche de

conglomérat avec le ciment calcaire, comblée des échinides et des nummulites. Les nummulites sont lavés, naturellement préparés et on les trouve en grand nombre sur la surface, tandis que les échinides sont disposés chaotiquement à l'intérieur du gisement. Leur position est différente par rapport au gisement, mais dans la plupart des cas ils sont retournés par la face aborale en haut, ou ils sont, dans certaine mesure obliques. On les trouve très rarement la face orale retournée en haut. Les relations réciproques et densité sur l'unité de la surface varient sensiblement. Quelquefois ils sont tellement resserrés qu'ils se touchent par la moindre ou de la plus grande partie de squelette et forment la masse fondamentale du gisement. Les cailloux roulés sont ceux qui predominent ailleurs, tandis que les squelettes des échinides se trouvent dans une position subordonnée. Les exemplaires de dimensions différentes se trouvent côte à côte non assortis d'après leur grandeur (fig. 1 a, b).

Quant à la faune accompagnante concentrée dans le gisement même ce ne sont que des rares représentants des lamellibranches et des gastropodes.

Parmi les échinides ce sont les représentants du genre *Conoclypeus* qui prédominent. D'après le nombre d'individus ils sont représentés avec 50% approximativement. Les représentants des genres: *Echinolampas*, *Linthia*, *Prenaster*, *Pericosmus*, *Cyclaster* et *Macropneustes* sont présent avec plus ou moins grand nombre d'espèces, et chaque espèce avec un nombre considérable d'individus. La liste complète des échinides déterminés appartenant à ce gisement se compose de 16 espèces: *Conoclypeus conoideus* (Leske), *C. pyrenaicus* Cotteau, *Echinolampas eurysomus* Agassiz, *E. calvimontanus* (Klein) Loriol, *Linthia vilanovae* Cotteau, *L. ducrocqui* Cotteau, *L. ybergensis* Loriol, *L. subglobosa* (Lamarck) Desor, *L. orbignyi* Cotteau, *L. inflata* (Desor) Cotteau, *Prenaster alpinus* Desor, *Pericosmus nicasei* Pomel, *P. spatangoides* (Desor) Loriol, *P. hispanicus* Cotteau, *Cyclaster ovalis* Cotteau, et *Macropneustes brissoides* (Leske) Desor. Neuf parmi elles sont caracteristiques pour l'Eocène moyen et sept autres indiquent seulement qu'il s'agit de l'Eocène, mais sans possibilité d'analyse précise. Comme la plupart des espèces indique l'Eocene moyen et comme on a trouvé un grand nombre de représentants de l'espèce *C. conoideus* — l'espèce très importante au point de vue biostratigraphique pour l'Eocène moyen on peut considérer l'âge de gisement comme celui de l'Eocène moyen.

Les conglomérats forment la base de la serie de flysche et leur épaisseur s'élève a 15 m environ. Au dessus d'eux on trouve alternativement les marnes argileux et les argiles, plus rarement les gisements calcaires, mais sans la faune (fig. 1c).

D'apres sa structure lithologique, ce flysche correspond absolument au flysche carbonatés. L'absence des grauwacke est caractéristique.

CARACTERISTIQUES PALEOECOLOGIQUES DE LA FAUNE ETUDIEE

La faune des échinides des conglomérats de la série du flysche du Pićan, au point de vue écologique est nettement hétérogène. Les représentants des genres *Conoclypeus* et *Echinolampas* avec des squelettes grands et massifs peuplaient, sans doute, le fond caillouteux. A en juger d'après le squellete tres grand et massif des *Conocylpeus* et d'après la présence des mâchoires (quoique tres réduites), ce genre était certainement située dans la zone littorale. La carapace grande et massive, resistait efficacement aux coups des vagues. La mâchoire quoique assez atrophiée permaittait une alimentation composée tout d'abord des plantes qu'on trouve surtout dans les régions littorales (algues de mer, herbes etc). L'*Echinolampas* presente encore un genre typique pour l'eau peu profonde. D'après J. Cottreau (1913) on rencontre les *Echinolampas* souvent dans la zone de *Litothamnium* qu'on peut comparer aux champs de *Zostera* dans la Méditerranée (a la profoundeur d'environ 30 m). T. Mortensen (1948) estime que les

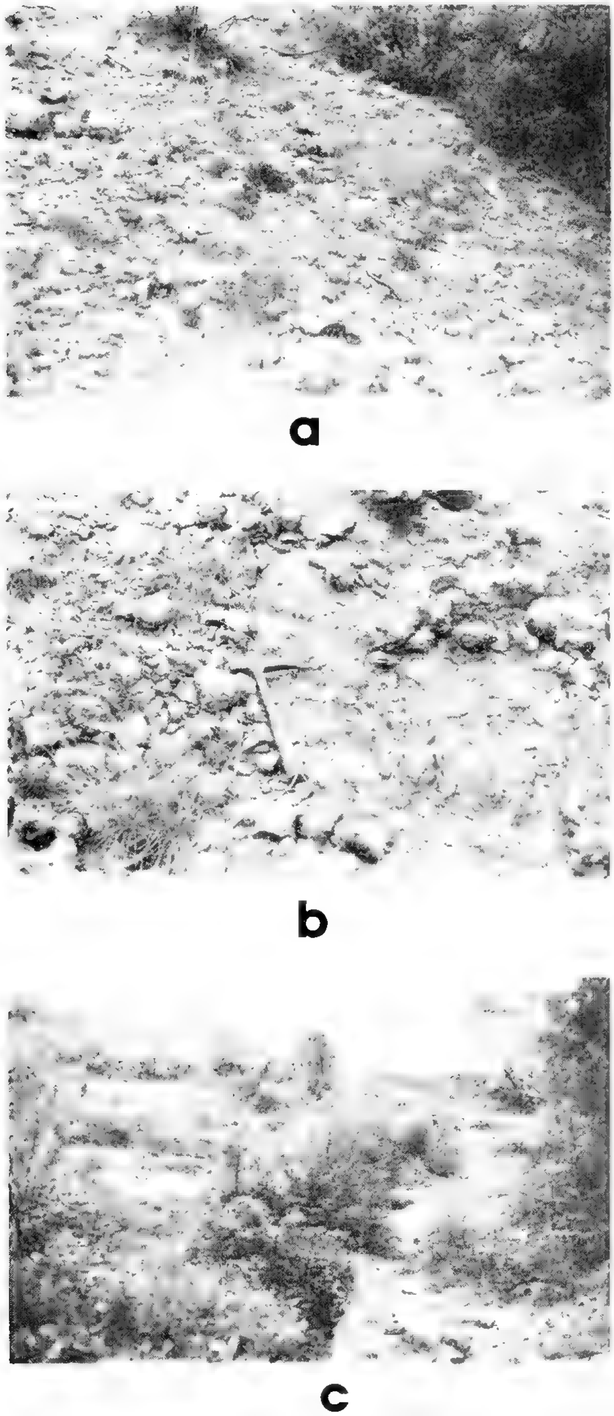

Fig. 1. **a.** Le gisement du conglomérat, **b.** Le gisement du conglomérat (detail), **c.** Le profil complet au-dessus de las source Bacva.

Echinolampas actuels sont trouvés dans les régions tropiques-subtropiques d'Atlantique et celles du Paciphique Indo-occidental, à la profoundeur de 10-500 m.

Les autres échinides, representants des genres: *Cylaster, Pericosmus, Linthia, Macropneustes, Prenaster*, avec les carapaces relativement tendres et fines habitaient un milieu un peu plus profound au fond vaseux. Leurs carapaces relativement fines et tendres, l'absence totale de la mâchoire, le labrum bien développé chez *Linthia* et *Pericosmus* témoignant une alimentation contenant la vase, tout cela sont des caractéristiques des échinides qui habitent l'eau un peu plus profonde. D'apres T. Mortensen (1951) les espèces actuelles du genre *Pericosmus* vivent au fond vaseux et gresseux à la profondeur de 18-486 m.

Un tres grand nombre de nummulites-foraminifères benthoniques de l'eau peu profonde témoigne de la petite profondeur de l'eau et de la proximité de la côte. Les gastropodes et les lamellibranches rares d'apres leurs caractéristiques morphologiques — les spires bases et les squelettes très gros des gastropodes, ainsi que les squelettes massifs avec une ornamentation très marqué chez les lamellibranches, témoignent aussi de l'eau peu profonde.

TYPES D'ENDOMMAGEMENTS LES PLUS FREQUENTS DE LA FAUNE DES ECHINIDES ETUDIEE

Les endommagements des squelettes résultent des facteurs chimiques, mécaniques et biologiques qui par leur action dans la mesure plus ou moins grande les produisent.

En ce moment les endommagements mécaniques provoques le plus souvent sous l'influence des vagues et des courants nous intéressent tout spécialement.

Les études de tels endommagements peuvent tres bien être appliquées en taphonomie, si l'on prend ce mot au sens plus large — comme un ensemble de facteurs qui ont influé sur la formation du gisements fossilifères.

Chaque élément de l'orictocénose peut donc être une source d'information sur les facteurs qui ont agi lors du passage de la biocénose à l'orictocénose.

La faune des échinides examinée dans l'ensemble est bien conservée, c'est à dire les squelettes sont en general tout entiers; proportionnellement il y a peu de squelettes cassés ou conservés fragmentairement.

On a remarqué pourtant les sortes différentes d'endommagements qui peuvent être classées en quelques types principaux:

1. Consomption-erosion du test. On y distingue plusieurs cas:
   (a) Le consomption approximativement uniforme de toute la surface due test avec les tubercules et les granules conservés encore, mais érodés considerablement.
   (b) Plus haut degré d'érosion du test dont le résultat est le manque presque complet des tubercules et des granules sur la plus grande partie du test. Ils ne sont conservés que sur les surfaces proportionnellement très petites et surtout sur la face orale.
   (c) Le plus haut degré d'érosion d'où résulte le manque total des tubercules et des granules.
2. Le manque, plus ou moins grand, du test d'où proviennent les dépressions plus ou moins profondes sur la surface du squelette. Dans certains cas il ne manque qu'un morceau du test, dans les autres il s'agit des depressions assez profondes.
3. Les fissures.
4. Les fracteurs qui ont emporté une partie du squelette la fragmentation.

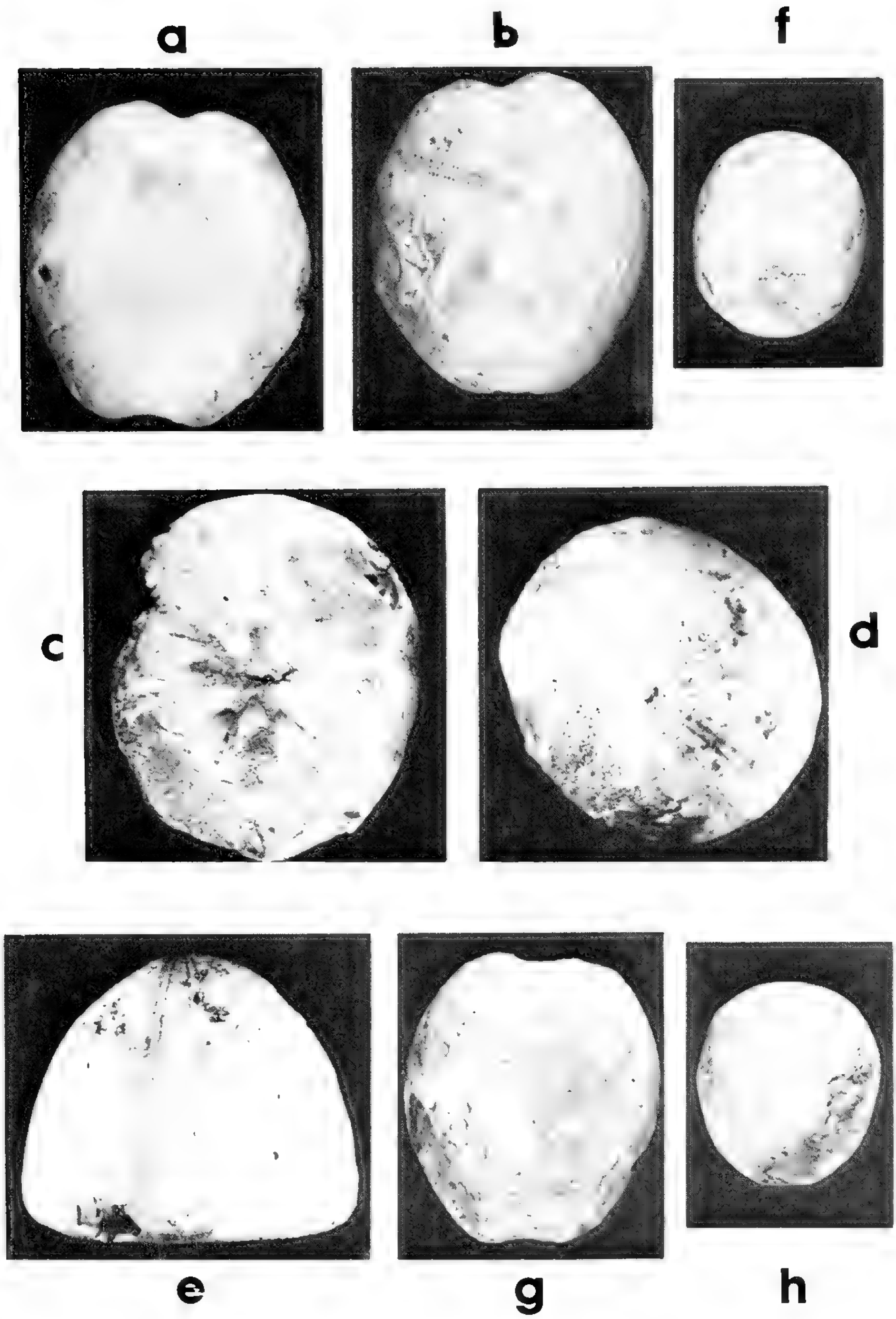

Fig. 2. **a-b.** *Macropneustes brissoides:* **a.** face orale, **b.** face aborale; **c-e.** *Conoclypeus conoideus:* **c.** face orale, **d.** face aborale, **e.** le profile; **f.** *Echinolampas calvimontanus* face aborale, on voit le manque d'une seule partie de test; **g.** *Macropneustes brissoides,* face aborale, on voit le manque d'une grande partie du test; **h.** *Cyclaster ovalis* face aborale, dépression remarquable sur la partie droite.

Parmi les types cités d'endommagement du squelette on rencontre le plus souvent le cas d'érosion plus haut ou les tubercules et les granules sont conservés sur les surfaces relativement petites et presque toujours uniquement sur la face orale, plus rarement au bord du test ou sur la face aborale dans la dépression d'ambulacre impair (*M. brissoides* fig. 2a,b).

A la deuxième place on peut citer le cas où l'érosion de la surface tout entière du test est plus ou moins uniforme, et les tubercules et les granules sont conservés encore, mais considérablement érodés. Autrement dit, l'ornamentation n'est pas en relief mais en même niveau avec la surface du test. Les tubercules et les granules sont nivelées ou bien on ne voit que leurs coupures. On trouve cela très souvent, surtout parmi les nombreux exemplaires d'espéce *C. conoideus* (fig. 2c,e).

Le manque d'une partie du test est aussi un phénomène fréquent. Jugeant d'après le nombre d'exemplaires ainsi endommagés, cette sorte d'endommagement occupe le troisième place. On peut distinguer deux cas fondamentaux: le manque d'une seule partie du test (plus rare) et les dépressions plus ou moins profondes (plus fréquent). Le premier cas est remarqué, par exemple chez les espèces: *Echinolampas calvimontanus* (fig. 2f), et *Conoclypeus conoideus* (fig. 2c,e). Le second cas est présent chez les nombreux exemplaires de beaucoup d'espèces: *Macropneustes brissoides* (fig. 2g), et *Pericosmus hispanicus*, *P. nicasei*, *Cyclaster ovalis*, *C. conoideus* et d'autres (fig. 2h).

Le plus haut dégré d'érosion d'où resulte le manque total des tubercules et des granules est aussi présent chez un nombre considérable de représentants: *Pericosmus nicasei*, *Linth. vilanovae* (fig. 3a,b), *L. inflata*, *Cyclaster declivis* et d'autres (fig. 3c,d).

On a rarement remarqué les fissures sur le matériel examiné. Chez quelques exemplaires de l'espèce *Conoclypus conoideus* la fissure oblique coupe la face orale et aborale dans la partie antérieur du test et elle est remplie de calcite, ce qui indique qu'elle provienne immédiatement après la mort de l'animal et qu'elle est remplie au cours du procès de la fossilisation (fig. 3e,f).

Enfin, le plus rarement on peut rencontre la fragmentation ou le manque total d'une partie du fossile. Ce phenomène est certainement la conséquence de la fracture arrivée immédiatement après la mort de l'animal ou pendant le transport (Fig. 3g,h).

DISCUSSION

Sur la base de tout ce qu'on a dit; des caractéristiques lithologiques du gisement fossilifère; de la position où la faune des échinides se trouve dans le rocher (relation vers le sédiment, relation réciproque, l'absence d'orientation absolue); de la grandeur des fossiles (les formes grandes et petites mélangées); du dégré et de la sorte d'endommagement du squelette (la faune proportionnellement bien conservée avec les endommagements uniquement sur les parties les plus exposées du squelette); les caractéristiques paléoécologiques de la faune des échinides et de la faune accompagnante; on peut conclure qu'il s'agit de l'orictocénose allochtone, mais que le transport n'a pas été long.

Quoique dans l'ensemble examinée l'association est allochtone elle continent une composante autochtone aussi. D'après leurs caractéristiques écologiques les genres *Conoclypeus* et *Echinolampas* seraient d'origine "in situ". Leurs tests massifs, ensuite la base élargie et solide et la présence de la mâchoire réduite chez les *Conoclypeus* permettaient la vie dans l'eau agitée dans le fond caillouteux.

Les représentants de tous les autres genres avec un squelette mince, un labrum bien développé, les ambulacres retirés dans les depressions indiquent la vie sur le fond argileux et dans l'eau un peu plus profonde.

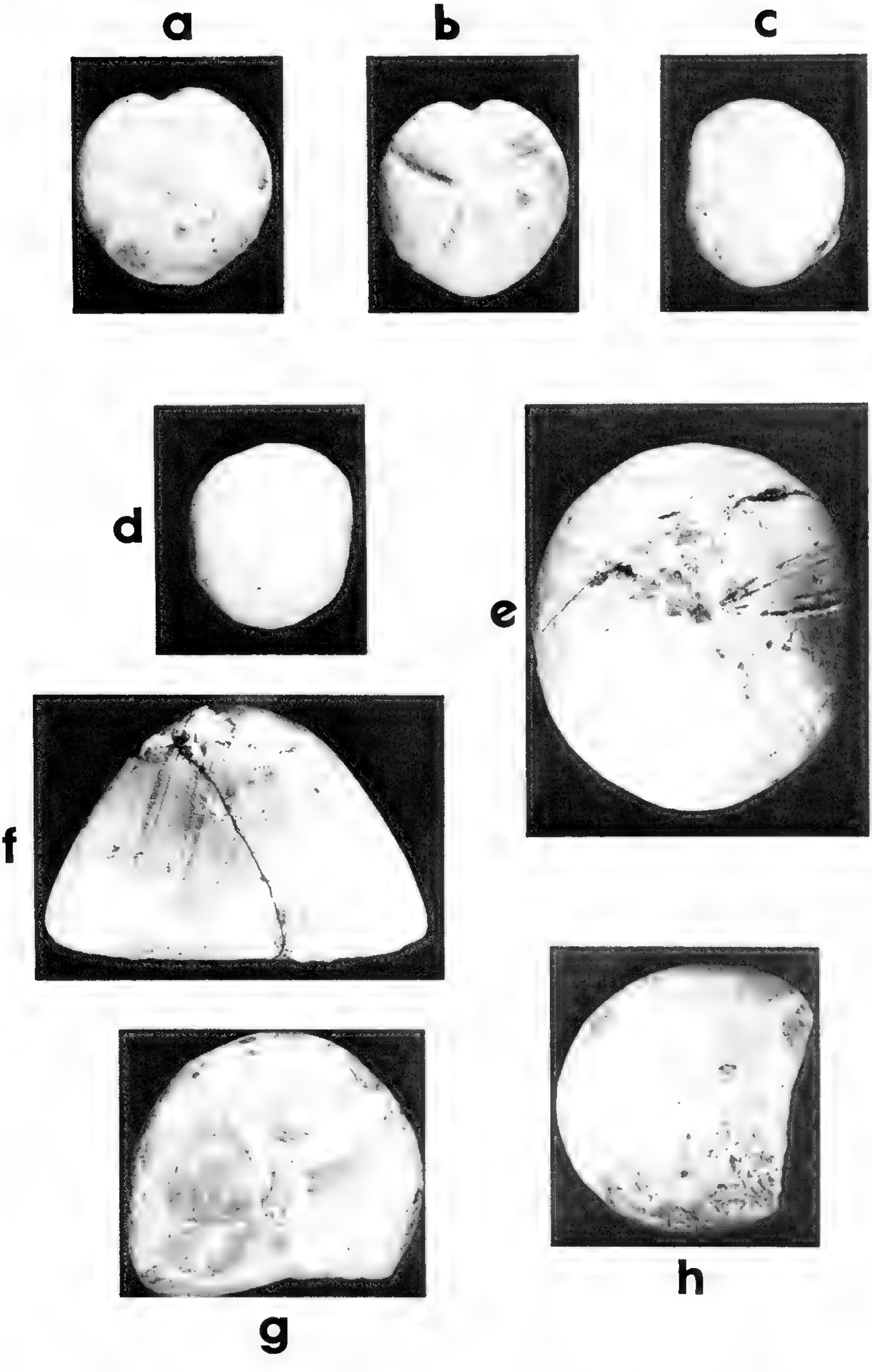

Fig. 3. **a-b.** *Linthia vilanovae:* **a.** face orale, **b.** face aborale; **c-d.** *Cyclaster declivis:* **c.** face orale, **d.** face aborale; **e-f.** *Conoclypeus conoideus:* **e.** face aborale, **f.** le profil; **g-h.** *Conoclypeus pyrenaicus:* **g.** face orale, **h.** face aborale.

La présence commune de ces deux groupes d'espèces des échinides liés aux fonds et aux conditions biotiques différentes résultent de la concentration secondaire de la faune sous l'influence "sediment flow" qui a apporté et redéposé les sédiments et la faune.

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2. ETUDE STRUCTURELLE ET FONCTIONNELLE DU TUBE DIGESTIF D'*ASTERIAS RUBENS* L. (ECHINODERMATA: ASTEROIDEA).

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SUMMARY

The digestive tract of *A. rubens* is composed of three morphologically and physiologically main regions: the floor of the cardiac stomach, the diverticula of the pyloric caeca and the rectal caeca. These regions are linked by transit zones (ciliary channels of the pouches and the upper part of the cardiac stomach, of the pyloric ducts, of the pyloric stomach and of the intestine).

During the meal the everted stomach — cardiac floor — is in intimate contact with the soft parts of the prey. The cardiac zymogen cells secrete their enzymes and extra-oral digestion occurs (extracellular digestion). Some particles of food are embedded in mucus and passed to the pyloric ducts by the ciliary channel of the cardiac stomach. At the same time the rectal current carries some small food particles directly into the rectal caeca where they are absorbed (intracellular digestion). The pyloric enzymes digest the food that has passed into the pyloric diverticula. The digestive products are then absorbed (extracullar and intracellular digestion).

The digestion by *Asterias* is virtually complete, little faecal matter being passed through the anus. Defecation is the result of the contraction of the rectal caeca wall, associated with the relaxing of the anal sphincter. The average duration of a meal is between five and six hours.

INTRODUCTION

L'anatomie digestive des astérides, particulièrement celles des Asteriidae (*Asterias, Marthasterias, Pisaster* . . .), est bien connue (Hamann, 1885, Cuenot, 1887 et 1948, Chadwick, 1923, Hyman, 1955 . . .). A l'opposé notre connaissance des structures microscopiques et/ou des fonctions de certains organes digestifs est encore assez fragmentaire. Des quatre principaux organes digestifs, ce sont les caecums pyloriques qui ont été le plus étudiés. On sait qu'ils sont un site d'élaboration et de sécrétion d'enzymes digestives (voir entre autres Sawano, 1936, Anderson, 1966, Peng et Williams, 1973). Leur structure histologique ainsi que leurs rôles dans l'absorption et la mise en réserve de nutriments ont été clairement établis par Anderson (1953). Les caecums rectaux sont également des organes absorbants (Jangoux, 1972 et 1976). La structure de l'estomac cardiaque des Asteriidae est surtout connue par le travail d'Anderson (1954) et l'estomac pylorique à été décrit de façon succincte par Jangoux *et al.* (1972).

Le présent travail récapitule et complète les notions acquises sur l'organisation digestive d'*A. rubens*. Le but poursuivi est d'établir un schéma fonctionnel de l'appareil digestif de cette espèce.

MATERIEL ET METHODES

Les *A. rubens* ont été récoltés sur un brise-lames de la côte belge à Knokke. Elles ont été gardées en captivité dans un aquarium marin en circuit fermé.

Pour l'observation histologique et les tests histochimiques les différents organes digestifs ont été fixés au Bouin acétique ou au formol 10% tamponné à la neutralité. Les fragments d'organes sont ensuite enrobés soit à la paraffine 57-60° C et coupés à 7 μ, soit au polyéthylène glycol-nitrocellulose (PEG) et coupés à 10-12 μ (technique de Reid et Taylor 1964 pour la préservation des graisses).

Australian Museum Memoir No. 16, 1982, 17-38.

Le détail des colorations histologiques et des tests histochimiques effectués se trouve exposé dans les ouvrages de Gabe (1968) et Gantes et Jolles (1969): Hématoxyline couplée à la phloxine et au vert lumière (topographie), Trichrome de Masson (topographie), Hématoxyline phosphotungstique de Mallory (topographie), Acide périodique — Schiff (APS, mucosubstances), Bleu alcian pH 2.6 et 0.5 (BA, mucosubstances), Couplage APS-BA pH 2.6, Tetrazoréaction de Danielli (protéines), Noir Soudan B controlé par extraction à la pyridine (lipides).

Pour l'étude ultrastructurelle, de fins fragments d'organes sont fixés 30 min. à 4°C dans une solution de glutaraldéhyde (2 ml de glutaraldéhyde 6% 1 ml tampon cacodylate 0.4 M, 1 ml NaCl 7%). Après lavage dans le tampon (30 min.), ils sont postfixés 1 h à 4°C au tétroxyde d'Osmium (2 ml OsO_4 2%, 1 ml tampon cacodylate 0.4 M, 1 ml NaCl 10%) puis à nouveau lavés dans le tampon (15 min.) pour être enfin déshydratés dans de bains d'ethanol de degré croissant. L'inclusion se fait dans l'épon (Luft, 1961) ou l'araldite (Glauert et Glauert, 1958) et les coupes sont réaliseées à l'aide d'un ultramicrotome Reichert Om U2. Les coupes semi-fines (0.5 µm) sont colorées au bleu de toluidine ou au bleu de méthylène et observées en microscopie photonique. Les ultracoupes (± 400 A) sont recueillies sur grilles de cuivre (300 trous), contrastées a l'acétate d'uranyle et au plomb (Reynolds 1963) et observées au microscope électronique Philips EM 300.

Des observations *in vivo* et des vivisections ont permis de suivre les mouvements du tube digestif lors d'un repas. La détermination du sens des courants ciliaires digestifs a nécessité également des vivisections: des organes ou fragments d'organes vivants sont placés dans un milieu physiologique contenant une suspension de carmin ou d'encre de Chine et observés au binoculaire.

OBSERVATIONS ET RÉSULTATS

1. ANATOMIE DE L'APPAREIL DIGESTIF (fig. 1)

La bouche s'ouvre directement dans un vaste estomac subdivisé en deux étages: le cardia, ventral, et le pylore, dorsal. L'estomac cardiaque est une large cavité occupant les trois-cinquièmes du volume du disque de l'astérie. Il présente une symétrie pentaradiée par le développement de cinq poches radiales aux parois extrêmement plissées. Les poches cardiaques sont chacune rattachées aux vertèbres ambulacraires d'un bras par une paire de ligaments triangulaires. L'ensemble de ces ligaments forme le système rétracteur stomacal, système dont la nature (collagène, élastine et muscles) et le trajet furent étudiés en détail par Anderson (1954, *Asterias forbesi*). Les paires de ligaments prennent appui de part et d'autre des premières vertèbres ambulacraires et de là rejoignent le centre de chaque poche cardiaque au niveau d'une nodule. De chaque nodule partent ventralement des faisceaux accolés à la paroi stomacale et qui, après s'être plusieurs fois dichotomisés, s'enfoncent dans l'épaisseur du cardia. Ils fusionnent alors avec la couche conjonctivo-musculaire de l'organe. Les faisceaux accolés à la paroi stomacale forment le système rétracteur intrinsèque, les ligaments triangulaires constituant le système extrinsèque.

La configuration du système rétracteur permet de distinguer trois régions cardiaques. Il s'agit du plancher (portion comprise entre la bouche et la terminaison du système intrinsèque; oesophage *sensu lato*), des poches (portion recouverte du système intrinsèque) et du plafond cardiaque (portion comprise entre la région des nodules et l'étranglement du pylore). Lors d'un repas toute la partie du cardia comprise entre la bouche et la partie supérieure du système intrinseque peut s'évaginer, mais généralement l'évagination ne concerne que le plancher stomacal.

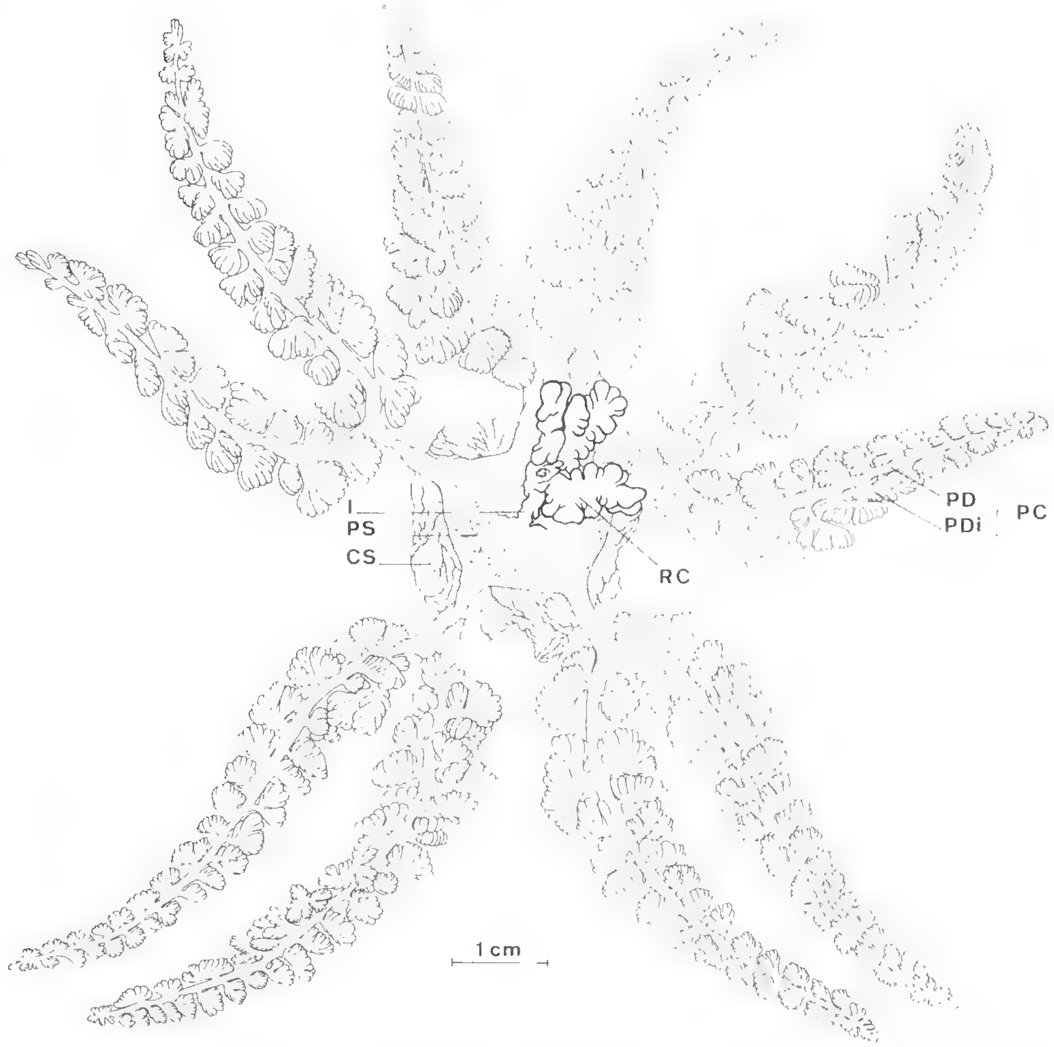


Fig. 1. Anatomie digestive d'*Asterias rubens*. CS = estomac cardiaque, I = intestin, PC = caecum pylorique, PD = canal pylorique, PDi = diverticule pylorique, PS = estomac pylorique, RC = caecum rectal.

Le pylore est séparé du cardia par un étranglement. La zone pylorique ventrale est d'un point de vue anatomique semblable au plafond du cardia dont elle est le prolongement direct. L'estomac pylorique se particularise d'avantage par une face dorsale pentagonale qui présente au contact de la lumière digestive une paroi lobée et très circonvoluée.

Chaque angle du pentagone pylorique donne naissance à un conduit de section ovalaire (canal pylorique) se dirigeant vers un bras. A la base des bras les cinq canaux pyloriques se dichotomisent et les dix canaux résultants donnent naissance à un caecum pylorique (deux caecums par bras). Les caecums pyloriques sont de longs appendices en cul-de-sac suspendus dans la cavité brachiale par chaque fois deux mésentères longitudinaux reliés à la paroi aborale du bras. Chaque caecum est formé d'un long canal médian qui n'est que la prolongation du canal

pylorique correspondant. Le canal caecal apparait comme une cavité comprimée latéralement et regulierement perforée. A chaque perforation correspond un diverticule pylorique, petite poche plurilobée et aveugle branchée sur le canal central.

Le très court intestin issu du pylore se jette dans les caecums rectaux en leur point de réunion. Ces caecums, au nombre de deux, sont rattachés à la paroi aborale du disque par un mésentere. Ce sont de petits sacs d'aspect variable. Extérieurement ils présentent de nombreux lobes, intérieurement ils envoient dans la lumière digestive de larges villosités. Un rectum à peine visible relie les caecums rectaux à l'anus.

2. HISTOLOGIE GÉNÉRALE

La structure de la paroi digestive est relativement constante. On distingue de dedans en dehors l'épithélium digestif, une zone nerveuse intraépithéliale (nerf interne, dépendance du nerf radiaire superficiel), du tissu conjonctif, une musculature parfois fort développée et à double orientation (circulaire et a longitudinale), des filets nerveux répartis dans la couche musculaire (nerf externe, dépendance du nerf radiaire profond) et un épithélium coelomique.

L'épithélium digestif est toujours la couche tissulaire la plus développée. C'est un épithélium monostratifié fait de cellules hautes et étroites (palissade). Toutes les cellules de revêtement sont ciliées et munies d'une bordure en brosse. Selon les organes elles acquièrent l'une ou l'autre spécialisation: production de courants d'eau, accumulation de produits de réserve . . . On distingue également différents types de cellules sécrétrices.

La zone nerveuse interne est assez discrète. On la remarque surtout sous les cellules épithéliales spécialisées dans la production de courants d'eau (plancher du cardia, canaux pyloriques, intestin . . .). Ailleurs elle est formée de fins prolongements axoniques s'immiscant entre les bases des cellules.

Le développement du tissu conjonctif est variable: particulièrement épais dans le plancher cardiaque et les caecums rectaux, il est quasi virtuel au niveau des diverticules pyloriques. La couche conjonctive est continue tout le long du tube digestif. Elle cloisonne de ce fait longitudinalement la paroi digestive et isole parfaitement le plexus nerveux superficiel du plexus nerveux profond.

L'importance de la couche musculaire varie également selon la région considérée. Lorsque la musculature est bien développée (plancher cardiaque et caecums rectaux surtout), elle se compose de plusieurs assises cellulaires et forme alors un tissu distinct de l'épithélium coelomique. Lorsqu'elle est faiblement développée (diverticules pyloriques par exemple), elle ne constitue plus une couche tissulaire distincte mais participe directement à la formation de l'épithélium coelomique (cellules myoépithéliales disposées entre les cellules épithéliales coelomiques). Le développement du plexus nerveux profond est directement lié à celui de la musculature.

L'épithélium coelomique se compose d'une rangée de petites cellules cubiques ciliées pourvues d'une collerette de microvillosités ("choanocyte-like cell" de Nørrevang et Wingstrand 1970). Ces cellules coiffent extérieurement la musculature digestive.

3. ESTOMAC CARDIAQUE

(a) **Plancher cardiaque.** C'est la portion du cardia comprise entre la bouche et les terminaisons du système rétracteur intrinsèque, elle correspond grosso-modo à la partie stomacale évaginable. L'épithélium digestif du plancher s'accompagne d'une zone nerveuse très importante. Le tissu conjonctif est ici particulièrement riche en fibres de collagène. La couche musculaire est bien développée et orientée longitudinalement; le nerf externe est développé en conséquence.

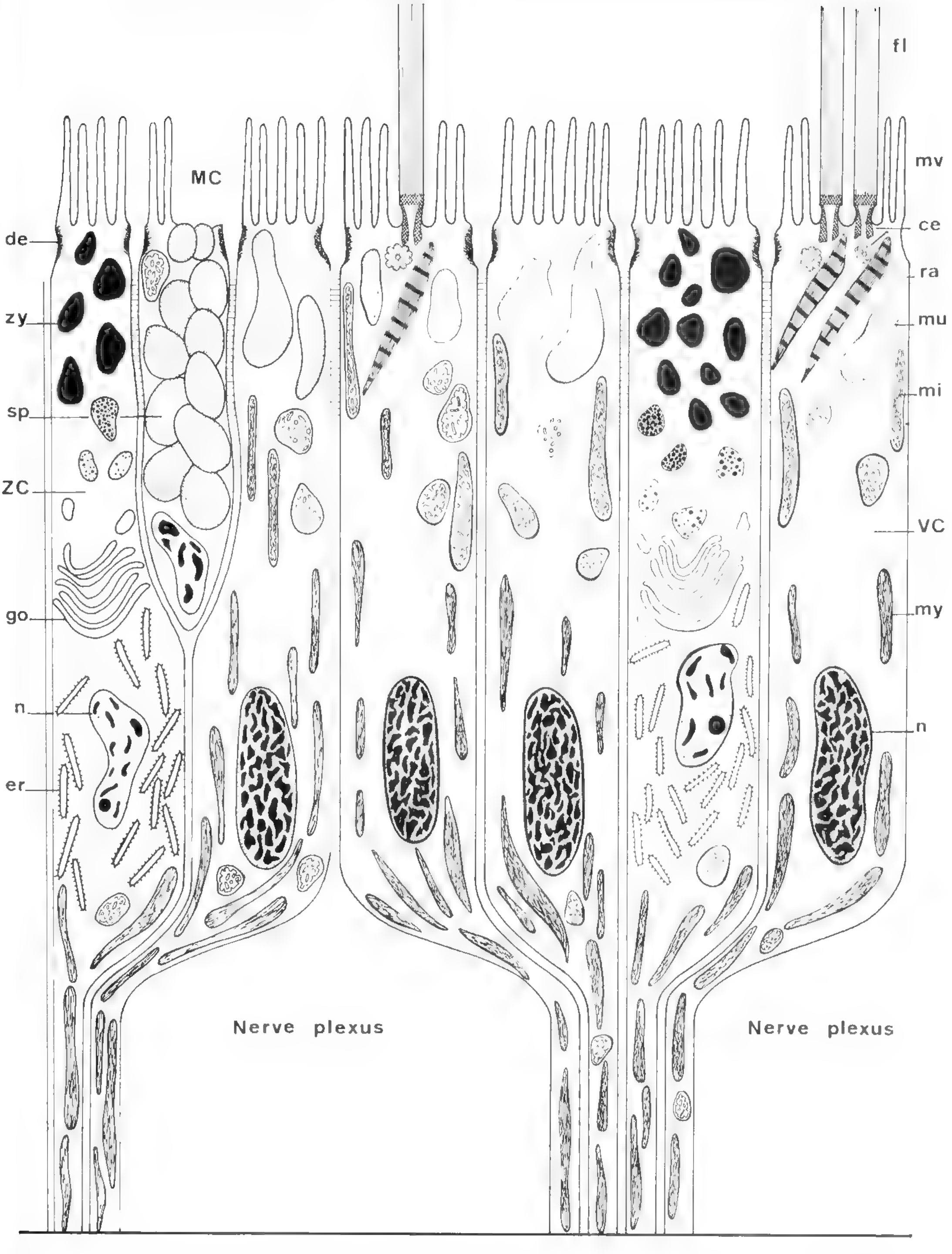


Fig. 2. Schéma de l'épithélium digestif du plancher cardiaque. ce = centrioles, de = desmosome, er = ergatoplasme, fl = cil, go = appareil de Golgi, MC = mucocyte, mi = mitochondrie, mu = plage muqueuse apicale, mv = microvillosités, my = myofibrilles, n = noyaux, ra = racine, sp = sphérule muqueux, VC = cellule vibratile, ZC = cellule zymogène, zy = granules zymogènes.

L'importance de la zone nerveuse interne confère à l'épithélium digestif du plancher un aspect remarquable. Les portions infranucléaires des cellules épithéliales sont en effet de largeur extrêmement réduite, elles forment de fins faisceaux d'ancrage attachant les cellules à la lame basale et entre lesquels s'étend le nerf interne (fig. 7c). Ces faisceaux renferment essentiellement des myofibrilles et quelques petites mitochondries, ils sont toujours en étroit contact avec des prolongements nerveux (fig. 7c). Les myofibrilles ne sont pas limitées à la portion infranucléaire des cellules, on les rencontre entourant et surmontant les noyaux, parfois même dans la région apicale (fig. 7a).

L'épithélium digestif du plancher renferme trois types cellulaires distincts: des cellules palissadiques, des cellules glandulaires spumeuses et des cellules glandulaires granuleuses (fig. 2 et 8a). Toutes présentent un amincissement infranucléaire et contiennent des myofibrilles. Elles sont en outre pourvues d'une bordure en brosse apicale et d'au moins un cil.

Les cellules palissadiques sont bien sûr de loin les plus nombreuses. Ce sont des cellules cylindriques, relativement étroites et munies d'une importante ciliature (2 à 5 cils par cellules). Il est certain qu'une de leurs fonctions est la production de courants d'eau, raison pour laquelle je propose de les nommer cellules vibratiles. Les cellules vibratiles sont attachées entre elles et aux deux autres types cellulaires par des desmosomes de deux sortes: des desmosomes classiques (*macula adhaerens*) visibles à l'apex et des desmosomes septés ne s'aperçevant que dans le tiers supérieur des cellules. Le cytoplasme apical des cellules vibratiles renferme trois éléments caractéristiques: des organites ciliaires basaux (centrioles, racine et microtubules), des mitochondries très allongées et une à deux plages muqueuses. Les organites cilaires sont tout à fait classiques. La présence à ce niveau de grandes mitochondries permet une activité ciliaire certainement très intense. Enfin les plages muqueuses, le plus souvent au nombre de deux, ont un contenu qui présente les réactions caractéristiques du mucus. L'épithélium du plancher est en réalité un épithélium glandulaire. Entre l'apex et le noyau le cytoplasme ne présente guère de particularités. Quant aux noyaux, leur forme allongée ("en cigare") et la forte densité de leur chromatine font qu'on les reconnaît aisément (fig. 7c).

On rencontre des cellules vibratiles à différents endroits du tube digestif. Elles se caractérisent toutes par l'existence d'au moins deux cils et la présence de longues mitochondries apicales. Leur noyau est toujours allongée, elles sont toujours amincies basalement et accompagnées d'une zone nerveuse bien développée. Les cellules vibratiles du plancher se différencient des autres cellules de même type par la présence de myofibrilles basales et de plages muqueuses apicales.

Les cellules glandulaires spumeuses, relativement nombreuses dans la région du plancher, ne sont rien d'autre que des mucocytes tout à fait typiques: leur sécrétat est constitué de mucopolysaccharides acides carboxylés et sulfatés. Mises à part les caractéristiques déjà citées (bordure en brosse, cil et myofibrilles basales) elles n'offrent pas de particularités. On les rencontre également en différents endroits du tube digestif, le plus souvent en association avec des cellules vibratiles.

Les cellules glandulaires granuleuses sont particulièrement intéréssantes. Moins nombreuses que les mucocytes on les trouve cependant sur toute l'étendue du plancher. Elles renferment de gros grains phloxinophiles qui s'avèrent être essentiellement de nature protéique. Observées au microscope électronique elles rappellent fortement les cellules zymogènes du pancréas de vertébrés (Berridge et Loschman, 1972). Elles présentent en effet un réticulum endoplasmique très développé, surtout dans la région infranucléaire, entre les saccules duquel se remarquent quelques petites mitochondries. Leur noyau se distingue nettement de celui des cellules vibratiles; il est de forme arrondie et a le nucléoplasme plus clair. Dans son voisinage s'aperçoit un volumineux appareil de Golgi formé de nombreuses cisternes et présentant des

vacuoles de condensation. Le contenu vacuolaire est de densité électronique variable et tout indique que ces vacuoles sont à l'origine des grains de sécrétion (fig. 7b). Ces derniers, présents en grand nombre dans la région apicale (fig. 7a), sont, rappelons-le, du nature protéique. Il est très vraisemblable que les cellules granuleuses du plancher cardiaque ont pour fonction de synthétiser et sécréter des enzymes digestives. Leurs caractéristiques ultrastructurelles permettent en tout cas de la supposer.

Il est certain que le plancher cardiaque occupe dans les phénomènes digestifs une place prépondérante. La composition cellulaire de son épithélium interne (fig. 2) ainsi que le fait qu'il entre très intimement en contact avec les zones digestibles des proies (évagination) l'indiquent à suffisance.

(b) **Poches cardiaques.** Les poches cardiaques correspondent à la région stomacale recouverte par les faisceaux conjonctivo-musculaires du système rétracteur intrinsèque. Elles sont au nombre de cinq et font légèrement saillie dans les cavités brachiales.

L'histologie des poches cardiaques est très différente de celle du plancher, au moins en ce qui concerne les tissus périphériques: la zone conjonctive et la couche musculaire sont fortement réduites sauf aux endroits ou s'accolent les faisceaux intrinsèques (fig. 8b). Les parois des poches sont extrêmement plissées, replis qui bien entendu s'atténuent voire disparaissent lors de l'évagination du plancher.

L'épithélium digestif des poches cardiaques renferme également trois types cellulaires: des cellules vibratiles, des cellules de revêtement banales et des mucocytes. Les cellules vibratiles des poches s'organisent en rubans orientés ventro-dorsalement: ils naissent de l'épithélium du plancher et se dirigent vers le haut. Au fur et à mesure que l'on s'éloigne du plancher le nombre de rubans vibratiles diminue progressivement par suite des fusions successives des rubans entre eux. Les cellules vibratiles forment ainsi de nombreux chemins ciliés au sein desquels se remarquent des mucocytes. Les cellules vibratiles des poches cardiaques sont accompagnées d'une zone nerveuse interne bien apparente (fig. 7d). Elles sont semblables à leurs consoeurs du plancher à ceci près qu'elles ne contiennent ni myofibrilles basales, ni plages muqueuses apicales. Entre les chemins ciliés, l'épithélium interne des poches est formé de cellules de revêtement banales ciliées (un cil), pourvues d'une bordure en brosse et dont la fonction essentielle semble être de faire palissade (fig. 7c, d). Les cellules banales sont plus larges que les cellules vibratiles et constituent de ce fait un épithélium d'aspect plus lâche.

(c) **Plafond cardiaque.** C'est la région comprise entre les nodules du système rétracteur et l'étranglement séparant le cardia du pylore. Mise à part la disparition des faisceaux intrinsèques, l'histologie du plafond cardiaque est semblable à celle des poches. Le nombre de chemins ciliés de l'épithélium interne diminue de plus en plus pour n'être plus que cinq au niveau de l'étranglement pylorique. Ces cinq chemins vont chacun contacter la gouttière ciliée ventrale d'un canal pylorique.

4. ESTOMAC PYLORIQUE (fig. 3)

L'estomac pylorique se particularise essentiellement par sa face dorsale très circonvoluée, la face ventrale n'étant rien d'autre qu'une zone de transition entre la plafond cardiaque et les canaux pyloriques.

L'histologie de l'estomac pylorique est relativement simple. L'épithélium digestif se compose de nombreuses bandes de cellules vibratiles et de mucocytes qui confluent toutes autour de l'orifice intestinal. Le trajet de ces bandes cilio-muqueuses s'observe très bien lorsqu'on regarde le pylore par son côté coelomique. Entre les chemins ciliés l'épithélium est formé de cellules de revêtement banales. L'épithélium digestif du pylore est très semblable à

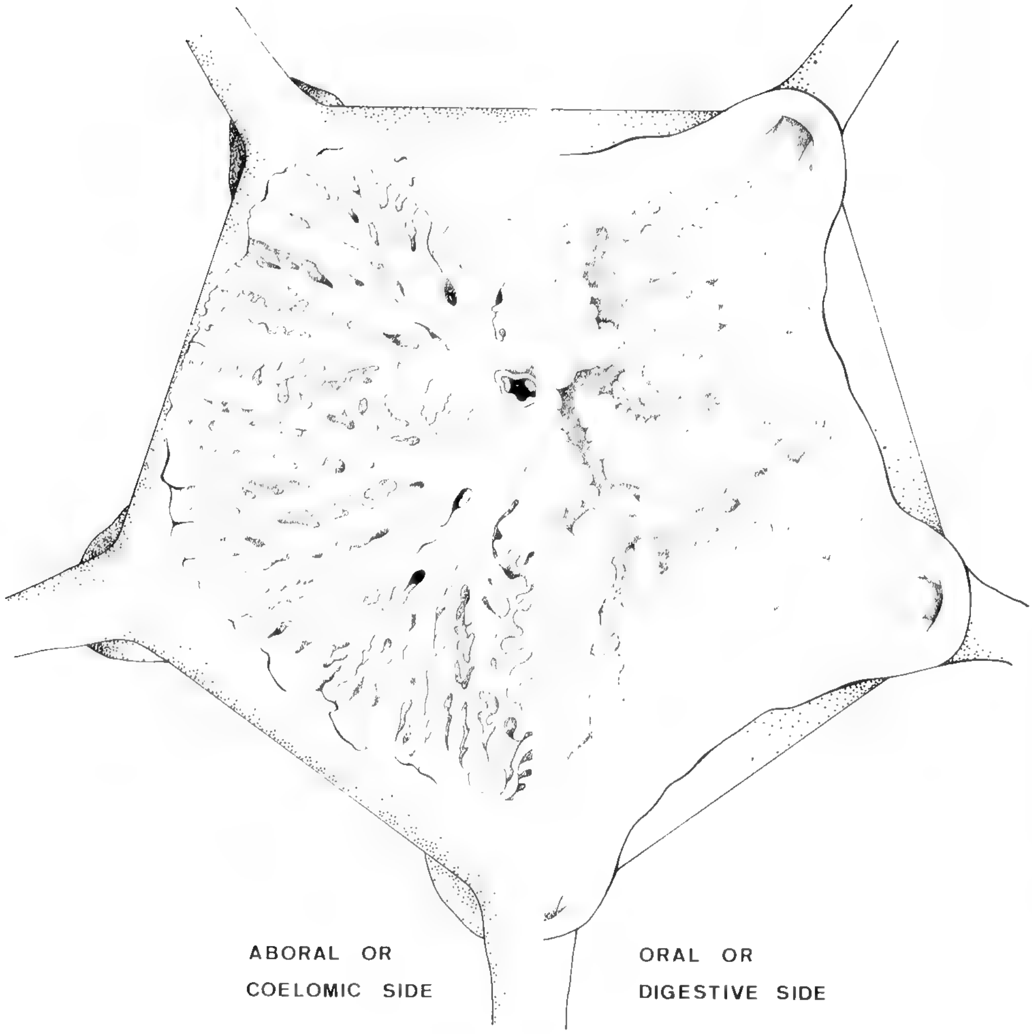


Fig. 3. Vues orale et aborale de l'estomac pylorique.

celui des poches cardiaques à ceci près que les bandes cilio-muqueuses sont ici plus nombreuses mais que leur ciliature est moins importante (rarement plus de deux cils par cellule). Le nerf interne est bien sûr très apparent et le conjonctif, d'épaisseur variable selon l'endroit, est riche de fibres collagène (fig. 9). La musculature est fortement réduite.

5. CANAL ET CAECUMS PYLORIQUES

Chaque canal pylorique donne naissance à deux caecums pyloriques. Chaque caecum se compose d'un canal central (portion caecale du canal pylorique) dans lequel se jette un grand nombre de diverticules pyloriques (figs. 1 et 4).

(a) **Canal pylorique.** La portion libre et la portion caecale du canal pylorique ont la même structure histologique. L'épithélium digestif est constitué par deux gouttières cilio-muqueuses (pôle oral et pôle aboral) séparées par des cellules de revêtement banales (paroi laterale). Le nerf

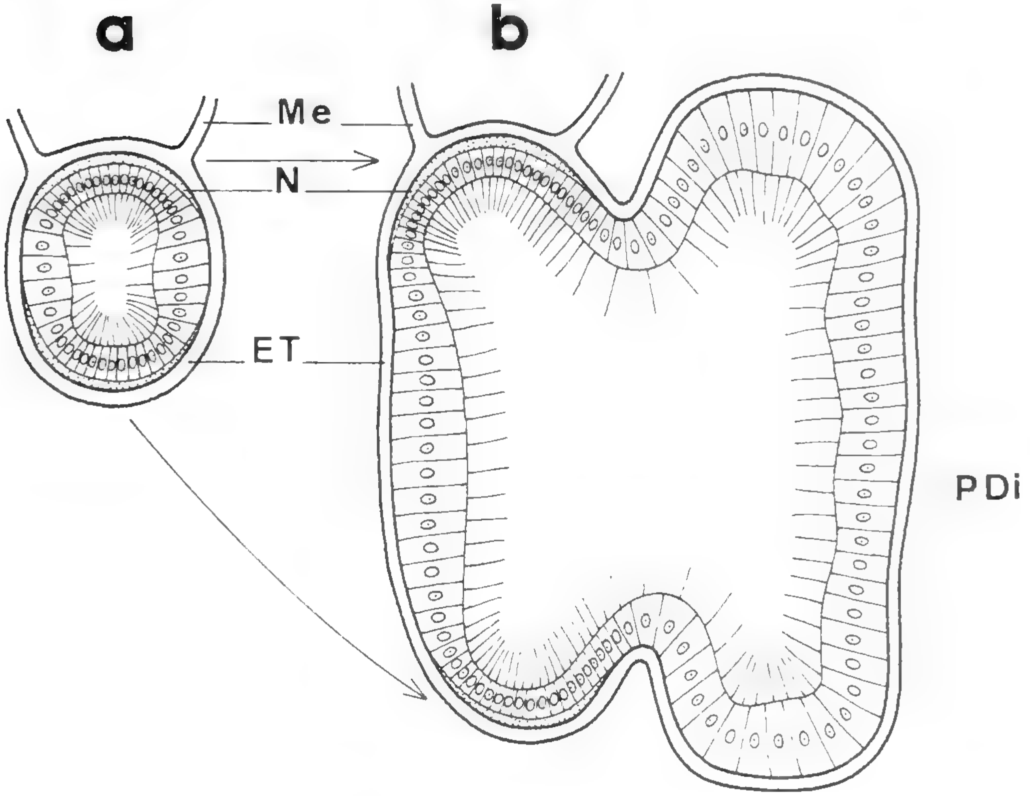


Fig. 4. Coupe transversale du canal (a) et du caecum (b) pyloriques. ET = tissus périphériques (conjonctif, muscles et épithélium coelomique), Me = mésentère, N = plexus nerveux, PDi = diverticule pylorique.

interne s'aperçoit au niveau des gouttières. Le conjonctif et la musculature sont peu développés. Le pôle aboral se distingue de son vis-à-vis par la présence de deux petites lacunes hémales situées dans le conjonctif au point de rencontre canal pylorique — mésentères d'attache.

(b) **Diverticules pyloriques.** L'épithélium digestif des diverticules pyloriques occupe plus des neuf-dixièmes de l'épaisseur de la paroi, les tissus périphériques sont extrêmement réduits (fig. 9c). Les caecums pyloriques ont été étudiés en détail (Anderson 1953, Nimitz 1971, Jangoux et Perpeet 1972) et leur composition cellulaire est bien connue. On y remarque des cellules de revêtement spécialisées dans l'accumulation de réserves énergétiques, des cellules zymogènes à large vacuole et, assez rarement, des mucocytes.

La fonction de réservoir énergétique des cellules de revêtement a été établie par Anderson (1953). Tout comme lui j'ai pu observer des goutelettes lipidiques et des granules de glycogène dans leur cytoplasme, principalement dans la région infranucléaire. Assez étonnamment il arrive que certains caecums soient dépourvus d'inclusions graisseuses et dans tous les cas il s'agit de caecums d'astéries récoltées en été. Cela s'explique par le fait que tant la quantité que la composition des réserves pyloriques varient au cours de l'année (Jangoux et Van Impe 1977).

Le noyau des cellules de réserve est arrondi ou légèrement ovale et renferme une trame chromatique lâche, rien ne le distingue du noyau des cellules de revêtement banales. Les cellules de réserve sont également absorbantes. Elles possèdent une bordure en brosse très serrée et le cytoplasme apical contient de nombreuses petites vesicules claires, résultat de l'activité pinocytaire (fig. 9b). On y remarque aussi quelques lysosomes et de petites mitochondries. Toutes les cellules de réserve sont ciliées (un cil).

Décrites pour la première fois par Anderson (1953), les cellules zymogenes des caecums pyloriques se caractérisent avant tout par la présence d'une large vacuole claire (fig. 9c). Cette vacuole semble vide et seules certaines préparations ultrastructurelles ont permis d'y observer un fin feutrage de nature inconnue. Le noyau est très reconnaissable par son gros nucléole central, il se place toujours sous la vacuole. Les grains protéiniques (grains zymogènes) s'observent sur toute le hauteur des cellules. Les organites responsables de leur fabrication sont localisés de façon plus précise, généralement au voisinage du noyau. Il n'est pas rare de rencontrer à cet endroit des complexes d'organites composés d'un appareil de Golgi, de saccules ergastoplasmiques et de mitochondries. Ces dernières entourent très souvent les grains zymogenes en formation. Les cellules zymogènes pyloriques sont ciliées et coiffées d'une bordure en brosse.

6. PARTIE POSTÉRIEURE DE TUBE DIGESTIF

(a) **Intestin.** Sa structure est particulierement simple. C'est un tres court conduit tapissé entièrement de cellules vibratiles parsemées de quelques mucocytes. Il reproduit l'organisation des bandes ciliées des poches et du plafond cardiaque, du pylore et des canaux pyloriques.

(b) **Caecums rectaux.** En coupe histologique les caecums rectaux se reconnaissement aisément: leur lumière est envahie de nombreuses villosités formées par l'épithélium interne (fig. 8e). Ces villosités sont sous-tendues par des lames conjonctives riches en fibres collagène. La musculature rectale est fortement développée et composée de deux couches de muscles d'orientations circulaire et longitudinale.

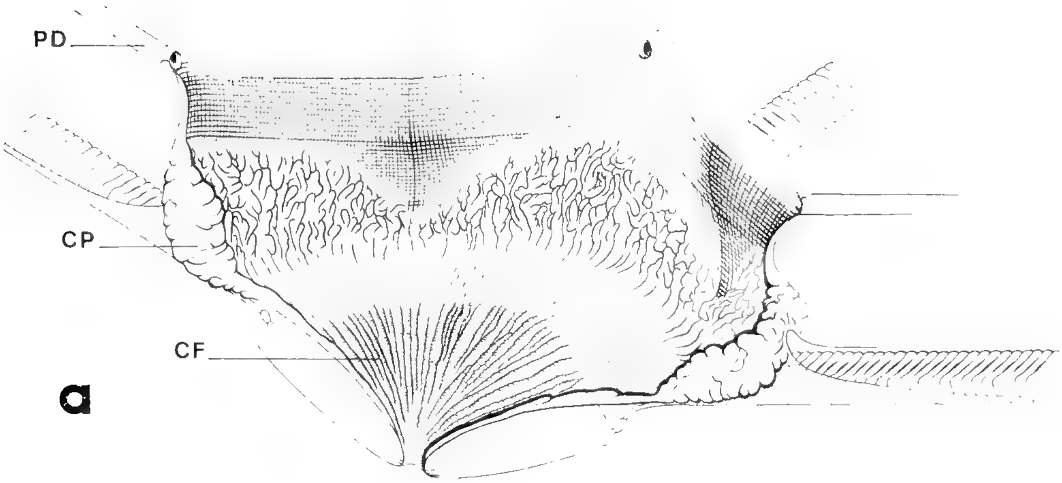
L'épithélium interne des caecums rectaux comprend deux types cellulaires: des mucocytes typiques et des cellules de revêtement d'aspect banal en microscopie photonique. L'étude ultrastructurelle des cellules de revêtement montre cependant qu'elles présentent de très intéressantes particularités (Jangoux 1972, 1976). L'existence d'une bordure en brosse serrée, de vésicules de pinocytoses et de lysosomes dans le cytoplasme apical indique qu'il s'agit de cellules absorbantes, fonction qu'elles partagent avec les cellules de réserve des diverticules pyloriques. Tout comme ces dernières elles sont ciliées. Toutefois, et à la différence de leurs homologues pyloriques, elles présentent de très longues mitochondries apicales. Le cytoplasme médian et le noyau, semblable à celui des cellules de revêtement cardiaques ou pyloriques, ne se caractérisent en rien. Par contre la zone cellulaire basale renferme d'importants replis membranaires (β-cytomembranes) limitant de fines bandes cytoplasmiques riches en mitochondries.

(c) **Rectum.** C'est un conduit tres fin et tres court. L'épithélium digestif n'est constitué que de cellules de revêtement banales. La seule particularité du rectum est l'existence d'une importante couche musculaire formant sphincter.

7. MOUVEMENTS DIGESTIFS LORS DU REPAS

(a) **Observations externes.** Le comportement d'une *Asterias* s'apprêtant à se nourrir est bien connu. L'astérie enserre la proie de ses bras et se bombe le dos du disque (réflexe du "gros-dos" ou "humping reflex"). Ce réflexe est très caractéristique et précède toujours l'évagination stomacale. Il peut également apparaître lorsqu'on place une astérie dans un milieu riche en aliments en suspension (Heeb 1973, Jangoux 1976).

L'évagination stomacale n'intéresse en général que le plancher cardiaque. Toutefois lorsque les proies sont de grande taille les extrémités ventrales des poches cardiaques peuvent faire saillie a l'extérieur. L'estomac évaginé ressemble à une vessie dilatée, gonflée de liquide coelomique sous pression. Cette surpression coelomique fait que lorsque le plancher cardiaque a pu s'immiscer entre les valves d'un bivalve par exemple, il se moule très exactement sur les



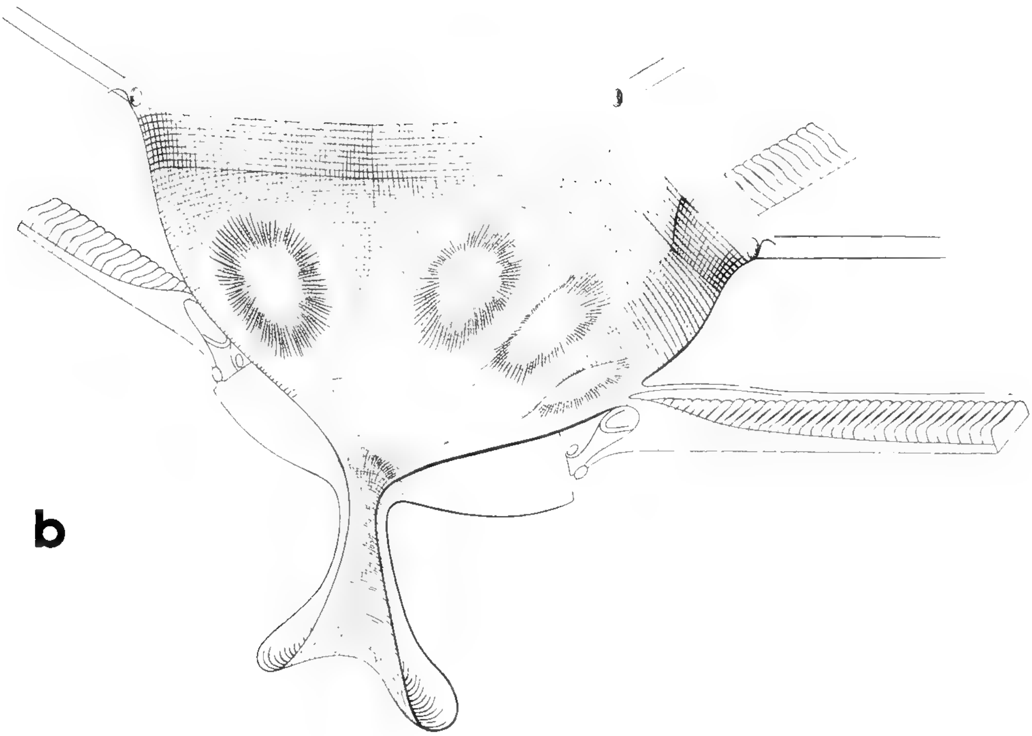


Fig. 5. Estomac cardiaque en place (**a**) et dévaginé (**b**). CF = plancher cardiaque, CP = poche cardiaque, PD = canal pylorique. Les replis stomacaux longitudinaux ne sont pas représentés sur le dessin b.

parties molles de sa proie et les contacte intimement. La durée de l'évagination est très variable et dépend bien sûr des tailles relatives de la proie et de l'étoile de mer. On peut cependant estimer le temps moyen d'évagination à 5-6 heures, l'estomac n'étant remis en place que lorsque la coquille est parfaitement vidée. Pendant toute la durée de l'évagination l'astérie reste étonnamment immobile et semble se concentrer entièrement sur son repas.

Durant tout le repas le dos du disque est bombé. Seule une observation patiente permet de remarquer de temps à autre l'éjection d'eau par l'anus. De tels rejets s'observant très rarement chez une astérie au repos; ils peuvent se voir avec une certaine fréquence chez les individus s'alimentant (2 à 6 éjections heure). L'eau ainsi rejetée n'est pas limpide mais renferme des fèces brunâtres d'aspect muqueux (Jangoux 1976).

(b) **Observations Internes.** Lors d'un repas deux régions digestives présentent des mouvements modifiant plus ou moins leur configuration: ce sont l'estomac cardiaque et les caecums rectaux.

Estomac Cardiaque. Le mécanisme de l'éversion stomacale a déjà été explicité par Anderson (1954). Cela se déroule comme suit: ouverture de la bouche, relâchement du système rétracteur stomacal et des muscles de la paroi de l'estomac, contraction des muscles de la paroi du corps entraînant une augmentation de la pression intracoelomique et l'évagination du plancher cardiaque. Anderson ne précise toutefois pas ce qui est à l'origine de l'étonnante extension de la paroi du plancher. Selon moi cette élasticité est principalement le résultat de la contraction des myofibrilles intraépithéliales (voir 3.a), ce qui permet l'étirement transversal de la paroi stomacale.

Il est évident que l'évagination stomacale modifie complètement la topographie du cardia (figs. 5, a et b). La modification la plus spectaculaire est bien sûr le considérable étirement du plancher cardiaque, mais la partie cachée de l'estomac va également changer de configuration. L'étranglement pylorique et les replis des poches du cardia s'estompent: poches cardiaques, plafond cardiaque et plancher pylorique s'alignent sur un même plan incliné allant de la bouche aux orifices des canaux pyloriques. La surface de ce plan incliné stomacal est couverte de chemins cilio-muqueux dirigés ventro-dorsalement et séparés par des plages de cellules banales.

Les mouvements stomacaux n'ont lieu qu'en début et en fin de repas. Pendant toute la durée de l'alimentation l'estomac reste "déroulé", tout au plus peut-on voir se modifier la longueur de la portion évaginée (contractions — relaxations des myofibrilles épithéliales).

Caecums Rectaux. Les seuls organes digestifs à présenter des mouvements répétés au cours d'un repas sont les caecums rectaux. Ce sont de petits organes contractiles aux parois très musculeuses. Leur contraction entraine un rejet anal d'eau (relâchement du sphincter rectal) et autorise donc la défécation. Des dissections d'étoiles de mer en train de s'alimenter ont permis de comprendre le fonctionnement des diverticules rectaux. Les deux caecums se comportent indépendamment l'un de l'autre, chacun est capable non seulement de se contracter mais aussi de se dilater très fortement. Lors d'un repas les caecums agissent en alternance de la façon suivante: alors que l'un d'eux semble au repos, l'autre se dilate très progressivement. La phase de dilation peut durer plusieurs dizaines de minutes, le caecum se gorgeant petit à petit d'un liquide brunâtre. Au bout d'un certain temps l'organe dilaté se contracte violemment et rejette son contenu par l'anus. A la suite de cela le deuxième caecum entame sa phase de dilatation, le premier se mettant au repos. Alors que la période de dilatation peut durer plusieurs dizaines de minutes, la contraction est très rapide et ne dépasse jamais 10 secondes.

Le mucus brunâtre qui s'accumule dans la lumière rectale provient pour une bonne part de la cavité stomacale. Cela se remarque fort bien en dissection où on observe très souvent la présence d'un film muqueux continu allant des parois cardiaques à l'intestin. Ce phénomène n'est explicable que si on admet qu'ils existe un courant d'eau, sorte de pompage rectal, allant

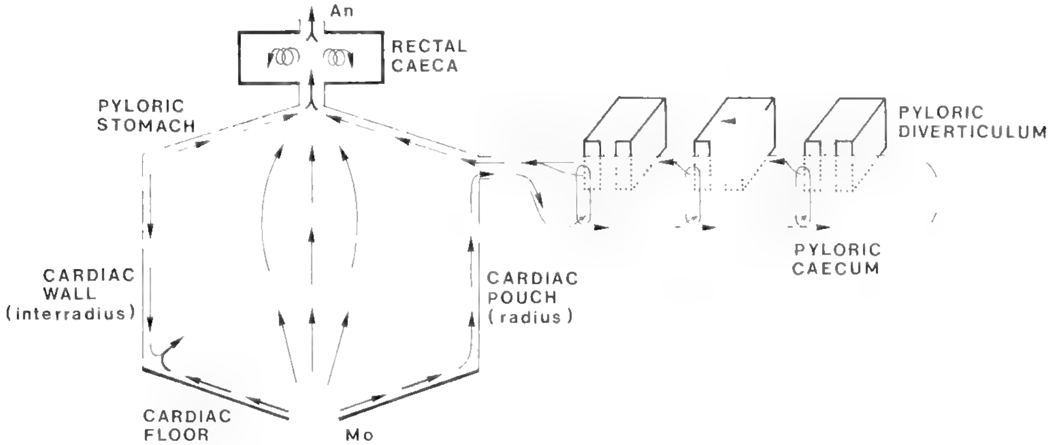


Fig. 6. Schéma fonctionnel de l'appareil digestif (en traits gras, les trois régions digestives principales). An = anus, Mo bouche.

dans le sens bouche-anus.

Le premier réflexe alimentaire significatif d'*Asterias* est celui du "gros-dos". Des dissections d'astéries au stade "gros-dos", c'est-à-dire avant l'évagination stomacale, ont permis de remarquer qu'un disque bombé renfermait toujours un caecum rectal dilaté. Il apparaît donc que le pompage rectal précède dans le temps l'évagination stomacale. La répétition de certaines des manipulations de Heeb (1973, adjonction dans l'eau de l'aquarium de diverses dilutions de broyat de moule) a montré que le réflexe du "gros-dos" n'est pas nécessairement suivi de l'évagination cardiaque. Celle-ci ne s'observera que si la dilution ajoutée au milieu est suffisamment concentrée en stimuli alimentaires. Le pompage rectal peut donc être déclenché lorsque l'astérie se trouve dans un milieu suffisamment riche en micro-aliments.

8. SENS DES COURANTS CILIAIRES

C'est au niveau des zones tapissées de cellules vibratiles que les courants sont les plus intenses. Leurs directions sont les suivantes (fig. 6):

— plancher cardiaque: courant ventro-dorsal
— bandes cilio-muqueuses des poches cardiaques, du plafond cardiaque et du plancher pylorique: courant ventro-dorsal
— plages de cellules banales des poches ou du plafond cardiaques: courant faible latéral ou dorso-ventral
— gouttière orale des canaux pyloriques: courant centrifuge
— gouttière aborale des canaux pyloriques: courant centripète
— diverticules pyloriques: courant tourbillonnaire
— bandes cilio-muqueuses du plafond pylorique: courant centripète
— intestin: courant ventro-dorsal
— caecums rectaux: courant tourbillonnaire

Ces résultats confirment et complètent ceux obtenus par Budington (1942) et Anderson (1954) sur *Asterias forbesi*.

DISCUSSION

Les cellules épithéliales digestives présentent deux caractéristiques fondamentales: elles sont en principe toutes ciliées (au moins un cil) et absorbantes (bordure en brosse). Cela ne signifie évidemment pas qu'il n'existe pas de sites absorbants privilégiés, sites qui sont les

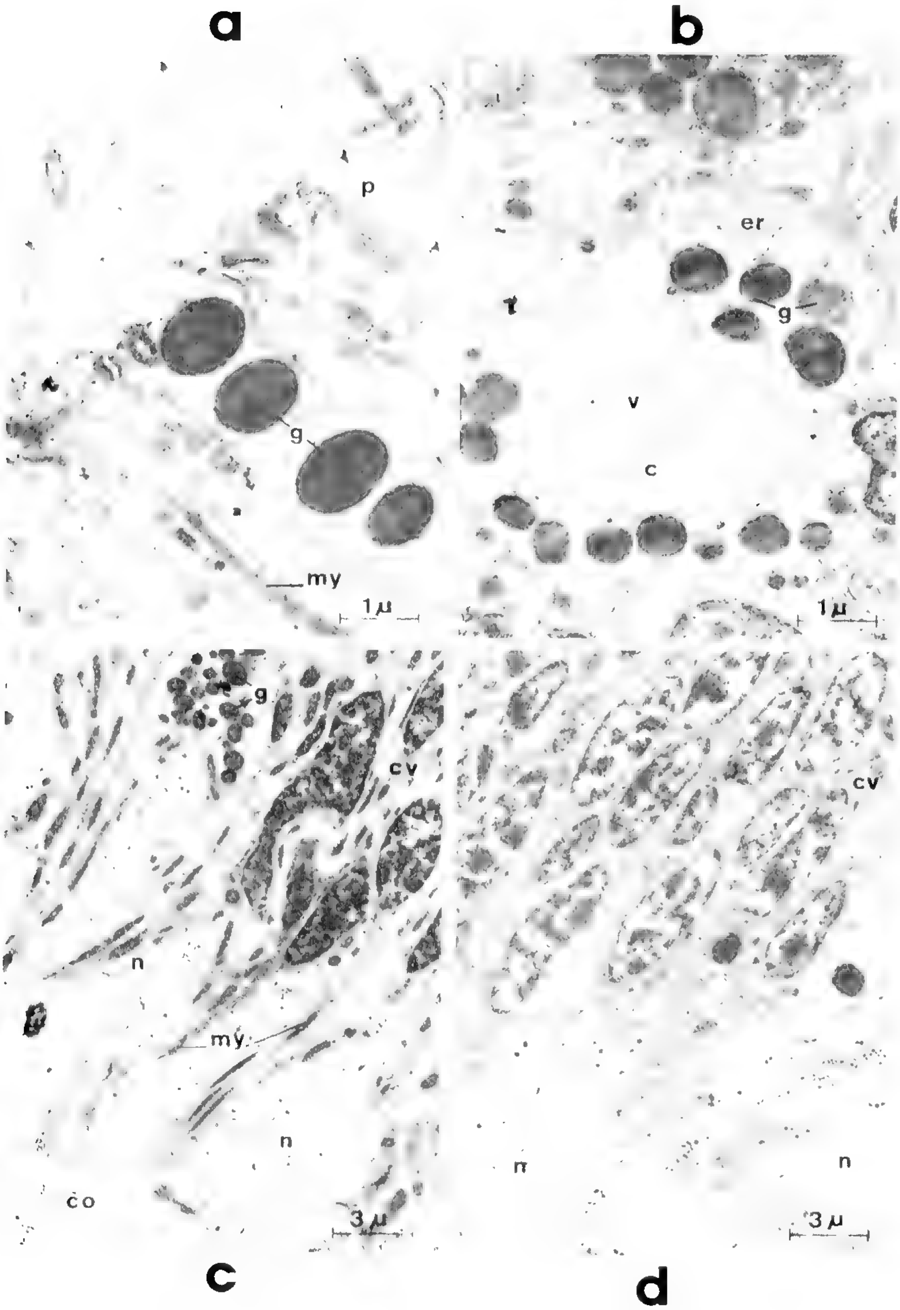


Fig. 7. Micrographies de la paroi du cardia (**a** à **c** plancher cardiaque, d poche cardiaque). (**a-b**) Cellules à grains protéiques (cellules zymogènes), c = cisternes de l'appareil de Golgi, er = ergastoplasme, g = granules protéiques (zymogènes), my = myofibrilles, p = plage muqueuse apicale d'une cellule vibratile; (**c-d**) = Base de l'épithélium digestif, co = tissu conjonctif, cv = cellule vibratile, g = granules protéiques (zymogènes), my = myofibrilles, n = plexus nerveux.

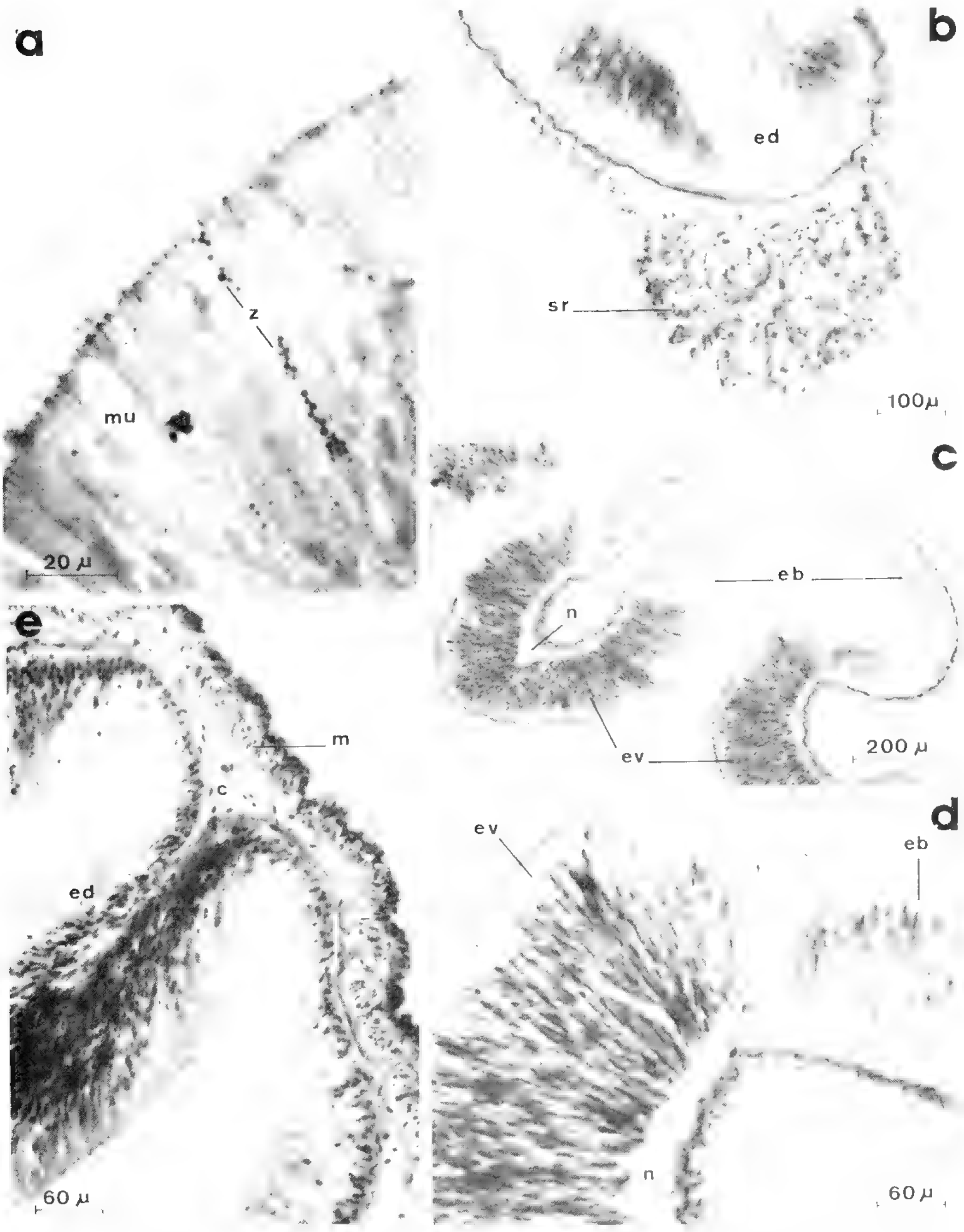


Fig. 8. Coupes transversales au travers du plancher (**a**) et des poches cardiaques (**b-d**), et des caecums rectaux (**e**). c = tissu conjonctif, eb = épithélium banal, ev = épithélium vibratile, ed = épithélium digestif, m = muscles, mu = mucocytes, n = plexus nerveux, sr = système rétracteur intrinsèque, z = cellule à grains protéiques (zymogènes).

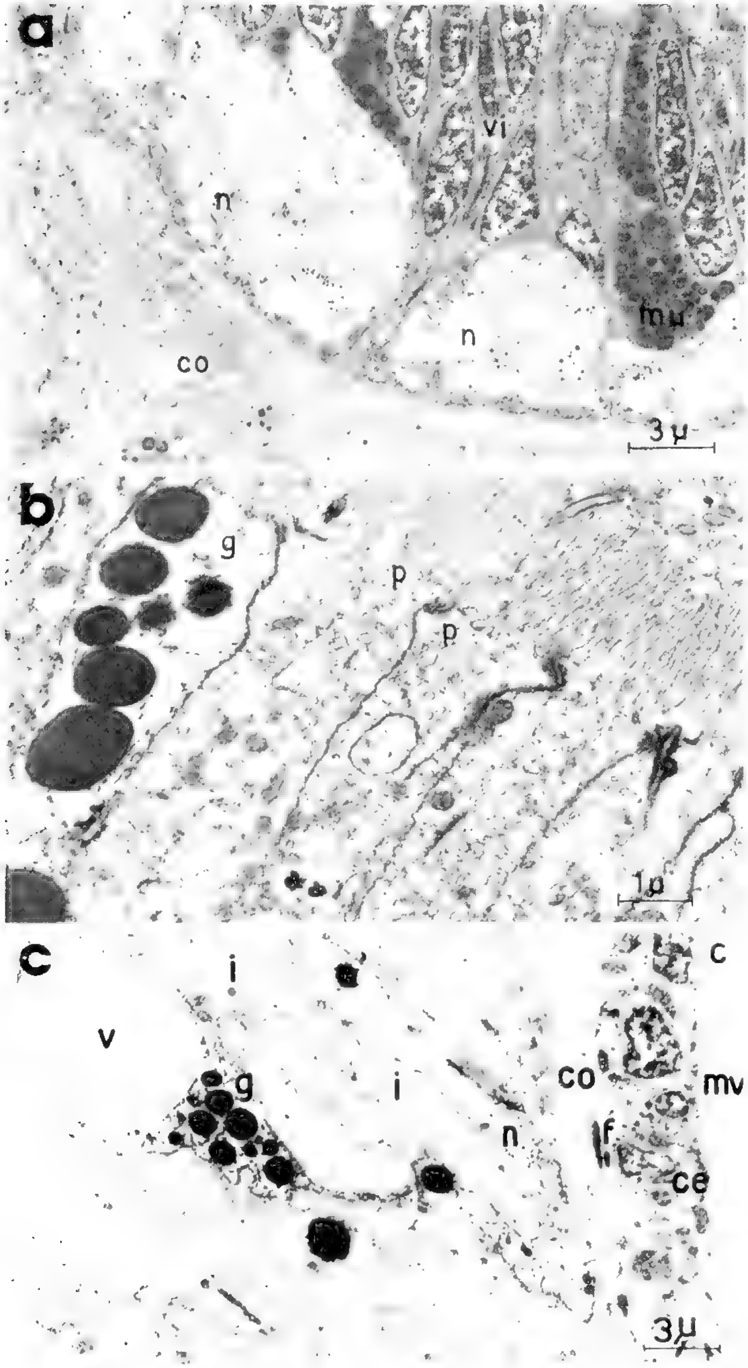


Fig. 9. Micrographies de la paroi du pylore (**a**) et de l'épithélium digestif des diverticules pyloriques (**b-c**). c = coelome, ce = épithélium coelomique, co = tissu conjonctif, f = fibres musculaires, g = granules zymogènes, i = inclusions lipidiques, mu = mucocytes, mv = microvillosités, n = tissu nerveux, p = vésicules de pinocytose, v = vacuole de cellule zymogène pylorique, vi = cellule vibratile.

caecums pyloriques et rectaux. Bien que composé de cellules diversement specialisees, l'épithélium digestif à un aspect semblable dans tous les organes: cellules hautes, étroites et assez serrées, formant une véritable palissade et rendant assez difficile l'observation microscopique. La microscopie électronique a permis de constater l'omniprésence du plexus nerveux interne dont les filets s'intercalent toujours entre la membrane basale et les membranes des cellules digestives. Le nerf interne est particulièrement bien apparent sous les bandes de cellules vibratiles; son trajet correspond à celui observé par Smith (1937) chez *Marthasterias glacialis*.

Le tissu conjonctif, riche en fibres de collagène, se développe différemment selon les régions. C'est au niveau des zones extensibles ou contractiles (plancher cardiaque et caecums rectaux) que son épaisseur est maximale. Le développement de la musculature digestive et du nerf externe qui l'innerve est parallèle à celui du tissu de soutien: le plancher cardiaque et les caecums rectaux sont les régions les plus musclées. Je rappellerai enfin que l'épithélium externe (coelomique) se compose de petites cellules cubiques ciliées et garnies d'une couronne de microvillosités ("chaoanocyte-like cells").

(a) **Estomac cardiaque.** Anderson (1954) s'est surtout attaché à étudier la structure du système rétracteur et des poches cardiaques, beaucoup moins celle du plancher du cardia (oesophage *sensu lato*). Les cellules à gros grains réfringents décrites par lui dans l'oesophage d'*A. forbesi* sont très vraisemblablement identiques aux cellules à grains protéiques du plancher cardiaque d'*A. rubens*. Par contre les cellules muriformes ("mulberry cells") observées par Anderson (1959) dans la paroi stomacale de *Patiria miniata* sont certainement d'un autre type; il s'agit probablement de coelomocytes.

Il est incontestable que le plancher cardiaque est la région stomacale la plus importante du point de vue digestif. C'est la partie évaginable et toutes les cellules épithéliales non glandulaires qui la constituent sont vibratiles (2 à 5 cils par cellule). Le fort courant ciliaire qu'elles produisent est unidirectionnel, et entraîne l'eau et son contenu vers les organes digestifs internes. L'estomac évaginé contacte très intimement les parties molles des proies: Anderson (1966) nous dit que l'espace séparant l'estomac de la proie est microscopique, pour ma part j'en estimerais la largeur à quelques dizaines de microns. Dans ces conditions le courant d'eau produit par les cellules épithéliales est très étroitement canalisé, ce qui augmente évidemment son efficacité. Outre une ciliature intense, les cellules vibratiles sécrètent du mucus (plages muqueuses apicales): elles vont donc pouvoir enrober les fragments de proie en même temps qu'elles les véhiculent vers le reste du tube digestif.

Etant donné qu'il y a digestion extra-orale, il faut qu'au niveau du plancher parviennent des enzymes digestives. La ciliature de la partie stomacale évaginée créant un fort courant ventro-dorsal, il est physiquement impossible que les enzymes nécessaires proviennent des caecums pyloriques. Il est donc logique, en dehors de toute observation microscopique, de supposer l'existence de cellules zymogènes dans le plancher cardiaque. Cette supposition est vérifiée par l'étude histologique et ultrastructurale qui y a révélé la présence de cellules à grains protéiques présentent les caractéristiques classiques des cellules zymogènes. Ces cellules sont d'ailleurs très semblables aux cellules gastriques exocrines observées dans la première spire digestive de l'oursin *Strongylocentrotus* par Holland et Lauritis (1968). En conclusion on peut penser que chez *A. rubens* le phénomène de la digestion extra-orale se réalise exclusivement à l'intervention d'enzymes digestives originaires du plancher de l'estomac cardiaque.

Il convient ici d'insister sur une particularité propre à toutes les cellules de l'épithélium digestif du plancher: la présence de myofibrilles dans leur cytoplasme. Les contractions de ces myofibrilles permettent d'expliquer la remarquable élasticité du plancher stomacal, élasticité que la seule sur-pression du liquide coelomique ne pouvait expliquer (la surpression étant essentiellement responsable de la turgescence de l'estomac évaginé).

Les poches et le plafond cardiaque ne sont importants que par les chemins cilio-muqueux qui les tapissent. Ce sont, avec la face ventrale de l'estomac pylorique, des zones de transition dont le rôle est d'acheminer vers le pôle oral des canaux pyloriques les petits fragments de proie enrobés de mucus.

A l'état de repos les poches cardiaques sont extrêmement plissées. En coupe histologique elles apparaissent comme une succession de creux et de crêtes, ces dernieres étant toujours tapissées de cellules épithéliales vibratiles (Anderson 1954, Jangoux *et al.* 1972). A la suite de l'évagination les poches s'étirent et les replis s'estompent. Les chemins vibratiles sont à ce moment tous disposés sur un même plan et séparés les uns des autres par des zomes couvertes de cellules de revêtement banales.

(b) **Estomac pylorique.** On peut comparer la face dorsale du pylore à une roue à rayons, chaque rayon étant constitué par une bande de cellules ciliées. Les courants d'eau créés par les bandes ciliées se dirigent tous vers l'orifice intestinal, centre de la roue. L'estomac pylorique est donc également un organe de transit. Dans le cas des Asteriidae, contrairement à ce que pensait Ferguson (1969), ce n'est pas le pylore qui distribue aux caecums pyloriques les produits de la digestion cardiaque. Ces produits leur sont en effet directement acheminés par les chemins ciliés du cardia. L'hypothèse de Ferguson est toutefois partiellement vraie dans la mesure ou les microparticules entrainées vers le haut par le courant rectal (courant buco-anal des caecums rectaux) peuvent être réceptionnées, enrobées de mucus et vehiculées par le pylore. Ces particules ne sont cependant pas destinées aux caecums pyloriques mais bien aux caecums rectaux, via l'intestin. En outre le pylore peut prendre en charge les matériaux rejetés par les caecums pyloriques (gouttière ciliée aborale des canaux pyloriques) et les diriger également vers les caecums rectaux.

(c) **Caecums pyloriques.** Les caecums pyloriques sont les organes digestifs les plus étudiés (Anderson 1953, Karnovsky *et al.* 1955, Bargmann et Behrens 1968, Chia 1969, Chan et Fontaine 1971, Nimitz 1971, Jangoux et Perpeet 1972). Ils sont formés d'un canal médian de section ovalaire (canal pylorique) parcouru par deux gouttières ciliées, l'une orale à courant centrifuge, l'autre aborale à courant centripède. Les parois latérales du canal pylorique présentent de part de d'autre et régulièrement des petits sacs plurilobés: les diverticules pyloriques. La gouttière orale alimente les diverticules en matériaux nutritifs originaires du cardia, la gouttiere aborale élimine vers le pylore les matériaux perdus ou refusés par les diverticules. Trois fonctions physiologiques importantes sont remplies par l'épithélium digestif des caecums pyloriques: l'absorption alimentaire, la mise en réserve de substances énergétiques, l'élaboration et la sécrétion d'enzymes digestives (voir entre autres Anderson 1966, Hori *et al.* 1977, Jangoux et Van impe 1977).

Comme permet de le penser la structure fine des cellules pyloriques et comme l'ont montré les expériences réalisées *in vitro* a l'aide de fragments de caecums pyloriques (incubation dans une solution marine de ferritine, Jangoux 1976), les cellules de réserve endocytent très activement. L'endocytose pylorique semble être discriminante et on peut supposer qu'une partie des matériaux rejetés par les caecums le sont à la suite de leur refus par les cellules épithéliales (Jangoux 1976).

Mise à part l'existence d'une large vacuole, les cellules zymogènes pyloriques offrent les mêmes caractéristiques générales que leurs homologues du plancher cardiaque. Cette vacuole n'est pas vide mais remplie d'un fin feutrage de nature encore inconnue. Le rôle de la vacuole reste mystérieux alors que la nature zymogene des grains de sécrétion à été clairement démontrée par Hori *et al.* (1977). Les enzymes digestives produits par ces cellules agissent sur les matériaux acheminés dans les diverticules pyloriques par la gouttière orale; ces enzymes poursuivent donc la digestion stomacale. On l'a vu, il est physiquement impossible que les enzymes pyloriques

parviennent au plancher cardiaque, les sens des courants ciliaires s'y opposent.

(d) **Caecums rectaux.** Les fonctions des caecums rectaux ont été récemment discutées (Jangoux 1976). Ce sont des organes contractiles, leurs contractions ayant pour principal effet de permettre la défécation (contraction caecale couplée au relâchement du sphincter anal). Au cours du repas les phases de contraction alternent avec des phases de dilatation lente. C'est pendant les dilatations que les caecums rectaux se gorgent de substances diverses (particules assimilables, mucus d'origine cardiaque et/ou pylorique . . .). Contrairement à ce qui avait été supposé (Jangoux 1976), il est peu probable que les dilatations des caecums rectaux soient responsables de l'existence d'un courant d'eau buco-anal. Au contraire elles en seraient plus volontiers la conséquence. Le "pompage rectal" est selon toute vraisemblance le résultat de deux mécanismes distincts: (1) après contraction, le retour des caecums rectaux à l'état de repos (relâchement de la musculature des parois) entraîne un appel d'eau; (2) la très importante ciliature intestinale draine l'eau de la cavité stomacale vers les caecums rectaux, entraînant ainsi leur dilatation. En d'autres termes le pompage rectal serait principalement la conséquence de l'activité ciliaire de l'intestin (mécanisme de pompage ciliaire).

Le pouvour absorbant des caecums rectaux est très élevé et il s'y déroule une intense digestion intracellulaire. Contrairement a ce qui se passe dans les caecums pyloriques, l'endocytose rectale ne parait pas discriminante (Jangoux 1976).

(e) **La mécanique digestive d'A. rubens** (fig. 6). Après avoir localisé sa proie (une moule par exemple) l'astérie la contacte, l'enserre de ses bras et applique très intimement un grand nombre de ventouses ambulacraires sur ses valves. A ce stade l'astérie se bombe (le dos du disque) (dilatation des caecums rectaux, déclenchement du pompage rectal) et peu après débute l'évagination du plancher cardiaque. On peut penser que ces différents réflexes alimentaires (pompage rectal et évagination stomacale) sont le résultat de chemoréception.

Des le déclenchement du pompage rectal, les caecums rectaux peuvent recevoir un certain nombre de particules alimentaires mais c'est bien sur l'évagination stomacale qui permettra l'apport nutritif le plus important. L'évagination cardiaque est un processus complexe nécéssitant succèssivement l'ouverture de la bouche, la relâchement du systeme rétracteur stomacal ainsi que des muscles de la paroi du plancher cardiaque et la contraction des muscles de la paroi du corps (raidissement de l'astérie). Cette contraction va entrainer une surpression du liquide coelomique qui va pousser le plancher stomacal, poussée qui entraînera la saillie stomacale dans le milieu extérieur. L'estomac évaginé revêt l'aspect d'un lobe blanchâtre turgescent, il va s'appliquer tres étroitement sur les valves de la proie. La taille de l'estomac évaginé peut varier: c'est la conséquence des contractions-relaxations des myofibrilles intraépithéliales du plancher cardiaque.

La façon dont l'estomac pénetre entre les valves de la proie n'est pas tres bien comprise. Sans doute profite-t-il a la fois des échancrures naturellement présentes entre les deux valves et des tractions exercées par les pieds ambulacraires sur les valves pour les écarter (Nichols 1964, Péquignat 1970). Une fois l'échancrure repérée, l'estomac est poussé dans le bivalve par la pression du liquide coelomique et va se mouler très exactement sur les parties molles de la proie. A ce moment les cellules zymogenes cardiaques déversent leurs enzymes et la digestion stomacale extra-orale débute (digestion extracellulaire). Les fragments de proie libérés par les ferments digestifs sont enrobés de mucus par les cellules du plancher et dirigés vers les chemins ciliés des poches cardiaques qui les transporteront jusqu'au niveau des canaux pyloriques. Pendant ce temps la pompe rectale fonctionne et entraîne dans le courant qu'elle crée de trés fins fragments de proie qui alimenteront directement les caecums rectaux (digestion intracellulaire). Il n'est pas interdit de penser que le pompage rectal favorise également l'acheminement des fragments de proie le long des chemins ciliés du cardia. Arrivés dans les diverticules pyloriques,

les fragments de nourriture vont subir l'attaque des enzymes pyloriques et les produits de cette digestion seront absorbés (digestions extracellulaire et intracellulaire).

Comme l'a signalé MacBride (1909), la digestion de l'astérie est très complète et peu de matériaux sont rejetés par l'anus. Les substances défécées ont une double origine: mucus brunâtre provenant de l'estomac et matériels refusés ou perdus par les caecums pyloriques et rectaux. Ces substances s'accumulent dans la lumière des caecums rectaux et sont éliminés par l'anus à l'occasion d'une contraction rectale. La durée moyenne d'un repas est de 5 à 6 heures, la proie n'étant abandonnée que lorsque sa coquille est parfaitement nettoyée. On assiste alors à la remise en place de l'estomac: relâchement de la musculature des parois de corps et diminution de la pression intracoelomique, contraction du systéme rétracteur et des muscles du plancher cardiaque, fermeture de la bouche.

Le schéma de fonctionnement du tube digestif proposé ci-dessus a été établi à partir de l'étude d'*Asterias rubens*. Etant donné la grande homogénéité anatomique des Asteriidae, il est très probable qu'il puisse, à quelques détails près, s'appliquer à toutes les espèces de cette importante famille. A l'opposé je ne crois pas qu'on puisse l'étendre aux autres familles de la classe. Les structures digestives sont en effet très variées dans le groupe des étoiles de mer (voir entre autres Anderson 1960, 1966, 1978) et à chaque type morphologique correspond sans nul doute une mécanique digestive particulière. En conclusion on peut dire que le tube digestif des Asteriidae est formé de trois régions importantes par leurs caractéristiques morphologiques et physiologiques, régions où se déroule l'essentiel des phénomènes digestifs (plancher cardiaque, diverticules pyloriques et caecums rectaux). Ces régions sont reliées entre elles par des zone transit (chemins cilio-muqueux des poches et du plafond cardiaque, des canaux pyloriques, du pylore et de l'intestin).

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3. THE REPRODUCTION OF SOME ECHINODERMS FROM MACQUARIE ISLAND

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SUMMARY

Three species of starfish, *Anasterias directa* (Koehler), *Anasterias mawsoni* (Koehler), and *Cycethra macquariensis* Koehler, and one species of holothuroid, *Pseudopsolus macquariensis* (Dendy) were collected over a period of one year from rocky sub-littoral shores at Macquarie Island. Study of preserved collections showed that both *Anasterias* species and the holothuroid have a brooding mode of reproduction and distinct reproductive cycles. For *Cycethra macauariensis* no cyclic reproductive pattern was evident. Ovarian condition in *Cycethra macquariensis* suggested a non-pelagic development; however the mode of this development was not observed. In addition, examination of some specimens of *Pseudocnus laevigatus* (Verrill), *Trachythyone macphersonae* Pawson (holothuroids) and *Pseudechinus novaezealandiae* (Mortensen) (echinoid) showed a brooding habit in *Pseudocnus* and ovarian conditions that suggested non-pelagic larval development for *Trachythyone* and pelagic larval development for *Pseudechinus*.

INTRODUCTION

Apart from prerequisite taxonomic studies, collections of marine invertebrates in the sub-Antarctic regions have been examined mainly for zoogeographical interpretation and reports on general ecology. Collections have usually been made in summer months and records of reproduction have been restricted to descriptions of non-pelagic development, especially via brooding or ovoviviparity. Simpson (1977) lists sources for the above studies.

At Macquarie Island, systematic collections were made each month for one year of some echinoderms from littoral and sub-littoral zones on rocky shores, in order to determine reproductive cycles and to categorise the mode of larval development as either pelagic or non-pelagic.

Apart from some nearby rocky outcrops, Macquarie Island (54° 38' S; 158° 53' E; Fig. 1) is isolated in the Southern Ocean. For studies of marine invertebrates, Macquarie Island is important in that (a) it marks the limit of southerly ice-free littoral zones and (b) its oceanic isolation bridges a geographic gap in any comparisons of littoral invertebrates over all southern latitudes in the Australian region.

MATERIALS AND METHODS

Specimens of the asteroids *Anasterias mawsoni* (Koehler) and *Anasterias directa* (Koehler), and the holothuroid *Pseudopsolus macquariensis* (Dendy) were collected at approximately monthly intervals between March, 1968 and March, 1969.

Another asteroid, *Cycethra macquariensis* Koehler, was collected monthly over the same period but collections were not obtained in the months of May, June and November. Within the size category designated for each species (see later), the first five specimens of each sex were examined from each monthly collection.

Four specimens of the holothuroid *Pseudocnus laevigatus* (Verrill), ten specimens of

Australian Museum Memoir No. 16, 1982, 39-52.

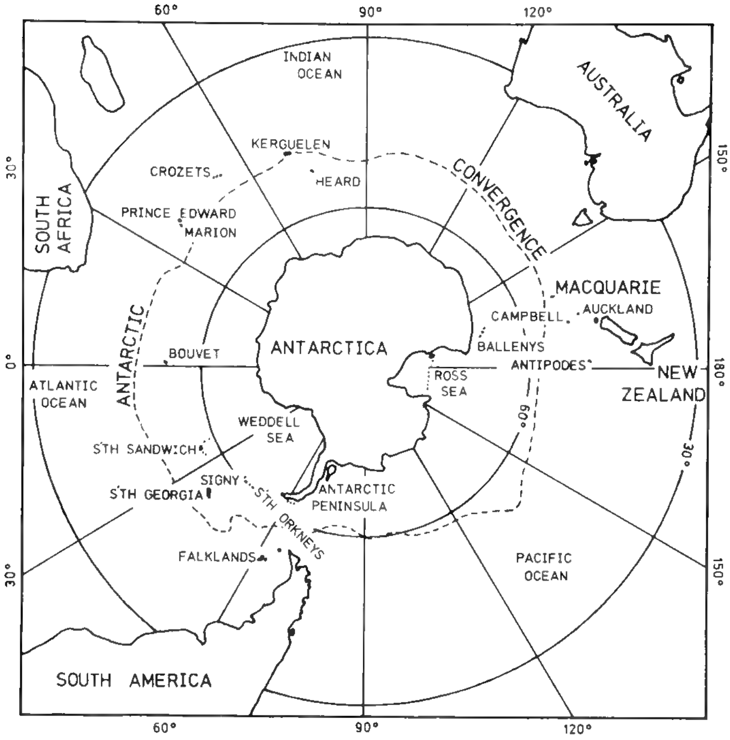

Fig. 1. The sub-Antarctic and Antarctic regions.

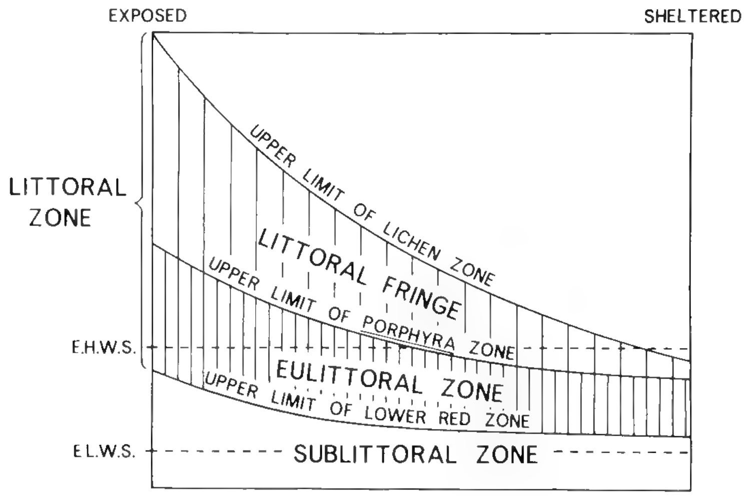

Fig. 2. Zonation of Macquarie Island rocky shores correlated with a universal scheme (from Simpson, 1976(a)). E.H.W.S.: extreme high-water spring tidal mark; E.L.W.S.: extreme low-water spring tidal mark.

Trachythyone macphersonae Pawson and four specimens of the echinoid *Pseudechinus novaezealandiae* (Mortensen) were examined for mode of reproduction only.

All specimens were preserved immediately after collection and the material was examined approximately one year after collecting ceased. The methods of preservation were those described in Simpson (1977). That paper also outlines the rationale, method, and terms used in describing the reproductive condition of a large collection of preserved specimens. The same procedures were applied, as appropriate, to the echinoderms. Briefly, for those species collected over a period of one year, reproductive conditions of specimens are described by egg sizes, the state of gonads and of broods, and stages in spermatogenesis determined by microscopic examination of smears of testes. An individual was labelled as being in a particular reproductive stage which, in most cases, was clear. When there was overlap (e.g. for spermatogenesis) the most predominant state was assigned as the stage for that individual. For the brooding species, progression in a brood was described by classification into eggs, embryos, and juveniles: eggs — when no embryonic differentiation was evident; embryos — when eggs showed embryonic differentiation; juveniles — when embryos appeared as fully formed juveniles.

The position of collecting sites was maintained by reference to the shore zonation scheme, as defined by Simpson (1976a), (see fig. 2). *Anasterias mawsoni*, *Anasterias directa*, *Cycethra macquariensis*, and *Pseudopsolus macquariensis* had a vertical range from the kelp zone of *Durvillea antarctica* (Chamisso) Hariot holdfasts in the lower eulittoral zone, down to a depth of 10 metres — the maximum depth investigated. Extension of the range of the above echinoderms up into the kelp zone depends on the cover provided by the living kelp (Simpson 1976a). While *Durvillea antarctica* itself could be classed as a lower eulittoral species, the zone it creates justifies a biological classification into a "sublittoral fringe". Both *Anasterias* had average densities on rocky surfaces of one per m^2 in the upper sub-littoral zone and two per m^2 in deeper water (Simpson, 1976b). *Pseudopsolus macquariensis* was often found in patches of high density on rocky surfaces. These patches were more common in the sub-littoral zone, and immediately below it, than in deeper water. *Cycethra macquariensis* was not abundant in any of the areas investigated.

RESULTS

Anasterias mawsoni (Koehler)

Anasterias mawsoni is endemic to Macquarie Island. It is a six-armed starfish and has a number of colour forms, any one specimen having a single colour. Distinctive features of this species are outlined in Clark (1962).

A. mawsoni was found on solid, rocky substrata. Specimens were collected from channels, gutters and pools at the top of the sub-littoral zone. All animals used for reproductive investigations had a central disc diameter of at least 20 mm.

The sexes are separate; out of 157 specimens sexed, 61 were males and 96 were females. A pair of gonads was situated in each of the six interbrachial regions. In the males, the testes had a botryoidal appearance while in the females each ovary consisted of two compact, round sacs. When ripe, the testes greatly enlarged and extended down into the arms; in the females, the sacs expanded to accommodate the enlarging eggs.

Figure 3 shows the annual reproductive cycle of *A. mawsoni*. The female brooded the young from egg to juvenile stage, the brood forming a compact cluster overlying the oral region (see fig. 4). Females assumed a distinctively arched posture when carrying a brood. The central disc was raised, the proximal parts of the arms being at a steep angle to the substratum and the distal parts horizontal and still attached to the substratum. This created a protected cavity at the oral

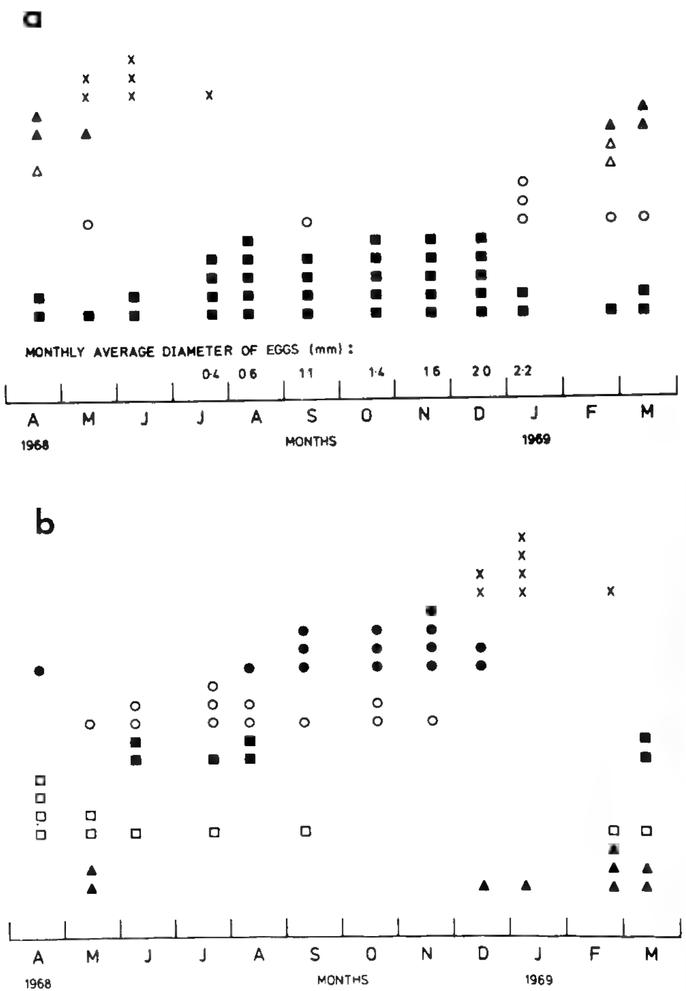

Fig. 3. Reproductive cycles of *Anasterias mawsoni*. **a.** females, N = 5 each month; X = evidence of recent juvenile release, ▲ = juveniles in brood, △ = embryos in brood, O = eggs in brood, ■ = eggs in ovary; **b.** males, N = 5 each month; X = recent spawning, ● = ripe, O = abundance of spermatids, ■ = early spermatogenesis, □ = resting, ▲ = resorbing. (Each symbol represents one specimen, the gonad of which has been classified by its predominant reproductive state. The sets of each symbol are stratified on the figure for better visual interpretation.)

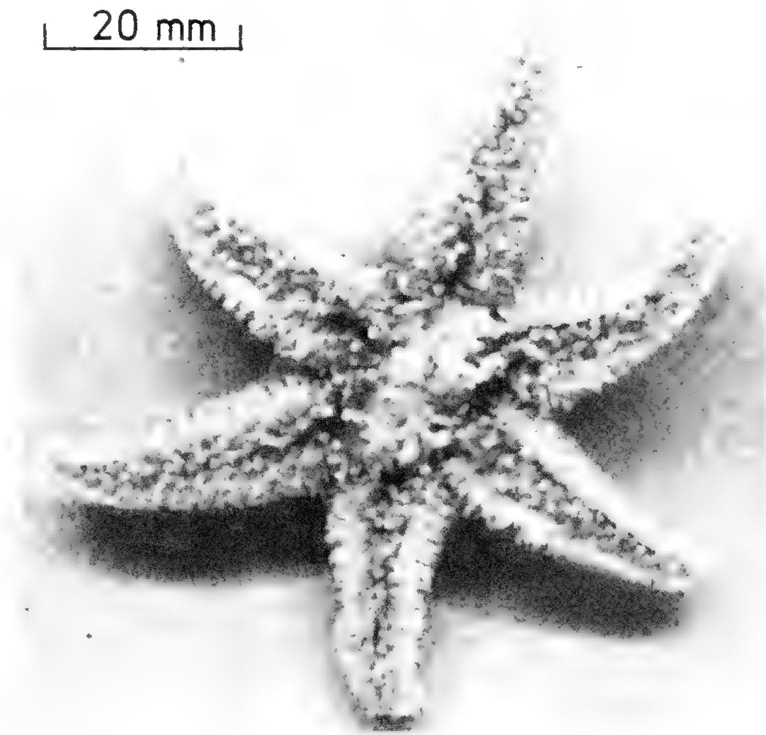

Fig. 4. *Anasterias mawsoni* with brood at juvenile stage.

region. Larger specimens could form a more spacious, protected cavity, and hence could presumably accommodate a larger brood. The number of eggs per brood varied from 168 to 296.

In July, the eggs in the ovaries averaged 0.4 mm in diameter. The eggs progressively increased in size, reaching 2.0 mm in December. They were transferred to the brood clusters in January-February at which time the diameter of eggs in a brood averaged 2.2 mm. Development proceeded in the brood to a juvenile stage in May and June when the juveniles were released. A female was classed in a "juvenile release" stage either when a very reduced brood was at the oral region or when there was no brood but there were membranous remnants of the brood sac around the oral region.

In males, the testes were generally reduced from February to May. There was some spermatogenic activity during this period, but occurrences were few. The testes then progressively increased in size and large, ripe testes were common from September to November. In December and January, they were reduced and mainly consisted of mature spermatozoa, indicating that spawning had recently occurred. The monthly reproductive conditions of the testes suggested that the breeding season occurred in early summer. During this period, the eggs were being transferred to the brood clusters.

Anasterias directa (Koehler)

Anasterias directa is endemic to Macquarie Island. It is a five-armed starfish and has a predominant dark olive colour form. Distinguishing features of the species are outlined in Clark (1962).

A. directa was found on solid, rocky substrata. Specimens were collected from channels, gutters, and pools at the top of the sub-littoral zone. All starfish used for reproductive investigations had a central disc diameter of at least 19 mm.

The sexes are separate. Out of 128 specimens sexed, 62 were females and 66 were males. A pair of gonads was situated in each of the five interbrachial regions. In the males, the testes had a botryoidal appearance, while in the females each ovary consisted of two compact round sacs. When ripe, the testes greatly enlarged and extended down into the arms. In the females, the sacs expanded to accommodate the enlarging eggs.

Figure 5 shows the annual reproductive cycle for *A. directa*. The female brooded the young from the egg to the juvenile stage, the brood forming a compact cluster overlying the oral region (see fig. 6). Small eggs were present in the ovaries in April and May, the average diameter in April being 0.5 mm. The diameter of the eggs increased to 1.1 mm in early June and progressively increased until they were transferred to a brood at the oral region in July, at which time diameter of the eggs ranged from 1.8 to 2.0 mm. Development of the embryos proceeded in the brood to a juvenile stage (October-November). The juveniles were released in the November-December period. Again, a female was classed in a "juvenile release" stage using the same criteria as for *A. mawsoni*. In January, the ovaries were small and the average egg size was 0.3 mm. The eggs progressively enlarged to an average diameter of 0.6 mm in mid-March.

In the specimens examined, the number of eggs per brood varied from 174 to 220, depending on the size of the starfish. Females exhibited a distinctively arched posture when carrying a brood (like that of *A. mawsoni*). Again, larger starfish were able to create a larger cavity and hence could accommodate a larger brood.

In males, during the corresponding period of brooding in the females, the testes were generally reduced in size and showed little signs of spermatogenic activity. Growth and spermatogenic activity were evident from November to February. Ripe testes were predominant in late February and March. They were present in April and May of the preceding year, but at

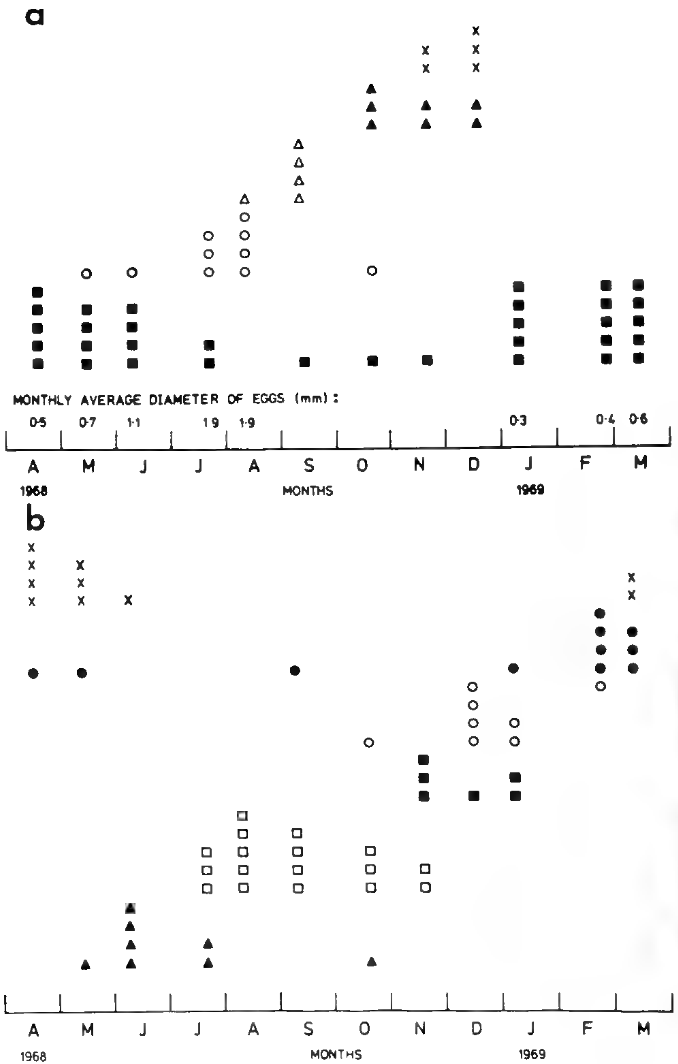

Fig. 5. Reproductive cycle of *Anasterias directa*. **a.** females, N = 5 each month; X = evidence of recent juvenile release, ▲ = juveniles in brood, △ = embryos in brood, O = eggs in brood, ■ = eggs in ovary; **b.** males, N = 5 each month; X = recent spawning, ● = ripe, O = abundance of spermatids, ■ = early spermatogenesis, □ = resting, ▲ = resorbing. (Each symbol represents one specimen, the gonad of which has been classified by its predominant reproductive state. The sets of each symbol are stratified on the figure for better visual interpretation).

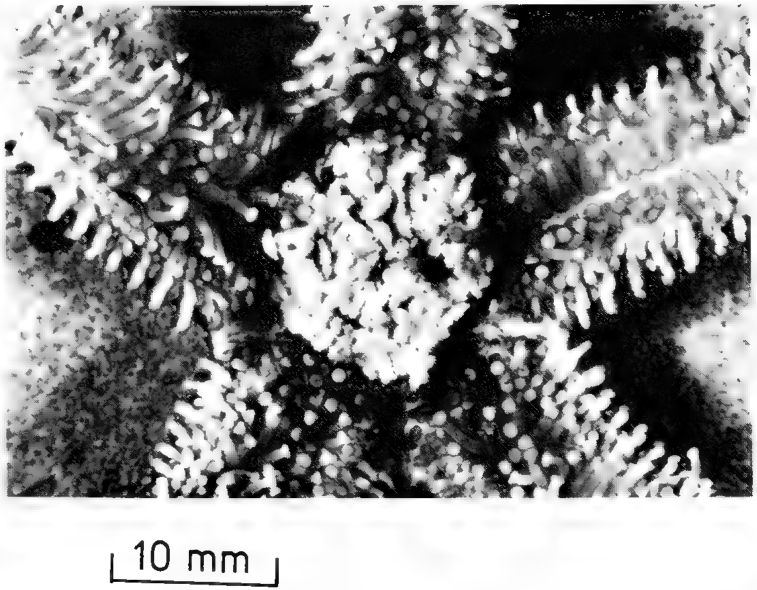

Fig. 6. Brood, at juvenile stage, of *Anasterias directa*.

this time testes were mainly reduced and consisted of mature spermatozoa with little signs of spermatogenic activity, indicating that spawning had recently occurred. The monthly reproductive conditions of the testes suggested a breeding season in the autumn. Yet, in this period, the eggs were still mainly held in the ovaries. From this pattern it appears that male spawning was too early if the eggs were to be fertilized during the seemingly opportune time of transfer to the brood region. Fertilization may occur in some other way. However, it is more likely that the above is a discrepancy in the pattern owing to either (a) a bias resulting from the small number of specimens used or (b) an ecologically-induced difference, that is, males being taken from habitats different to those of females in the first part of the collecting period (April-June).

Cycethra macquariensis Koehler

The nomenclature for this species is not clear. The collected specimens were firstly identified as *Asterina hamiltoni* Koehler. However, on examination of type specimens held by The Australian Museum, Sydney, the specimens from Macquarie Island were then identified as *Cycethra macquariensis* in the family Ganeriidae. Yet, on the basis of the arrangement of plates and spines, the specimens could be identified as a genus in the family Asterinidae, in accordance with the key in Clark (1962). Clark (1962) remarked that the separation between *Cycethra* and *Asterina* is indistinct.

Cycethra macquariensis is endemic to Macquarie Island. It is a small, five-armed starfish. Specimens were collected from pools and channels in the sub-littoral zone. All animals used for reproductive studies were at least 22 mm in total body diameter.

The sexes are separate. Out of 141 specimens sexed, 96 were male and 45 were female. A pair of gonads was situated in each of the five interbrachial regions. The testes had a botryoidal appearance and when ripe, were large and extended into the arms. Each ovary consisted of a number of small sacs (typically seven) and each sac contained eggs of various sizes. The number of eggs per sac varied from 19 to 24, the average being 20. There were three distinct size categories (diameter): (a) less than 0.3 mm, (b) 0.3 to 0.49 mm, and (c) 0.5 to 0.8 mm. The smallest eggs were more plentiful than the largest. In grouping the figures from all specimens, the range of numbers in the three size categories was (a) 11 to 16 ($\bar{x} = 13$), (b) 4 to 7 ($\bar{x} = 5$), (c) 1 to 3 ($\bar{x} = 2$).

The above condition of the ovaries was maintained throughout the collections. About 40% of the males had ripe testes in any one month. Thus *C. macquariensis* appeared to breed continuously throughout the year.

It is not clear whether females released ova to the sea for external fertilization. The average number of eggs per female is 20 x7 x 10 = 1,400 (number of eggs per sac x number of sacs per gonad x number of gonads). However, from the size range of the eggs, it was apparent that only about 140 of these were mature ova. The release of such a number would hardly ensure successful fertilization or survival rate if eggs were released to the open sea. No brood was found either enclosed in the body cavity or on the surface of the starfish. From the above evidence, it appears reasonable to assume that *Cycethra macquariensis* lays egg cases.

Pseudopsolus macquariensis (Dendy)

Pseudopsolus macquariensis is endemic to Macquarie Island. A description of the species is given by Pawson (1968). Specimens were collected from channels and gutters encrusted with coralline algae at the top of the sub-littoral zone. Adult holothuroids were commonly 25 mm long from the base of the tentacles to the anus. For plotting the reproductive pattern, specimens of at least 15 mm were used.

The gonad consists of a cluster of unbranched caeca uniting at a common base in mid-dorsal mesentery, approximately one quarter body length from the anterior end of the animal. From the base, a single genital duct passes to an opening in the oral disc. Ludwig (1898) grouped the caeca into left and right tufts, presumably using the mesentery wall as the divider.

The species has previously been described as hermaphroditic (Ludwig, 1898; Mortensen, 1925) but this requires further examination. For a maturing gonad, there are a number of large caeca that contain the developing gametogenic material which, for each animal, is either male or female — not both. (Any further designation here of an individual as male or female has used the sexual status of the large caeca as the criterion). The contentious point is the role of the smaller genital caeca at the base of the cluster. Ludwig (1898) described one specimen, which was obviously a male with a ripe gonad, and noted much smaller caeca containing "small eggs" 0.23 to 0.28 mm in diameter. In a description of two specimens, Mortensen (1925) reported a condition similar to that found by Ludwig in one and, in the other (a small female), he observed ovarian caeca each with two eggs (1.5 mm diameter) and some smaller caeca which he classed into both male and female types.

In the present study, 181 specimens (measuring 15 mm or more from anus to the base of the tentacles) were sexed as 102 males and 79 females. This bias in sex ratio was greater in a collection of 29 smaller specimens that were 12 to 15 mm in length (20 males, 8 females, 1 immature). Further observations on the 181 larger specimens showed that the small genital caeca were divisible into two groups: (1) very small buds and (2) caeca 1 to 3 mm in length which nearly aways contained egg-like forms. Four male specimens had small non-differentiated caeca containing spermatogenic material. Three specimens had developing ovarian caeca and thin, male caeca that were in a regressed stage. Two females with broods had genital caeca containing egg-like forms in some and, in others, developing testes arranged in a bead-like pattern down the caeca. These last five specimens confirmed the occurrence of successive hermaphroditism as reported by Ludwig (1898) and Mortensen (1925). However, the deductions on this point by Ludwig and Mortensen were ill-founded in using the presence of smaller genital caeca with egg-like forms to indicate that the next sexual role would be female. Such caeca appear to contain precursor material for either male or female formation. Histological work on specimens in key reproductive stages is required for further elucidation of such a process.

It is unlikely that each individual would change sex each year with a resultant switch in the sexual bias. This was confirmed by a similar state of sexual bias showing at both the start and end of the period of collection, which covered two successive reproductive cycles (see later). Thus, some individuals must retain the same sex in successive cycles. If sex change is an option for an animal, there is the speculative hypothesis that the number of females increases in response to some form of feedback that favours a population increase, and vice versa.

In a description of 8 specimens (11 to 19 mm in length) of a new sub-species, *Pseudopsolus macquariensis gruai*, from the Kerguelen Islands, Cherbonnier (1974) found gonads with 4 to 5 thick, white, male caeca and "about ten" very fine, long tubules with a "few eggs" less than a micron in diameter. Such a gonadal condition was not found in specimens of *Pseudopsolus macquariensis* in the present study.

The number of large caeca varied from 12 to 24 in both males and females. The caeca were divided into two groups by mid-dorsal mesentery usually with half the number in each group. Smaller caeca and buds at the base of the gonadal cluster were more numerous. When sexually ripe, large male caeca were looped and the total length of some exceeded the body length of the animal. In females, the number of eggs in caeca varied from 73 to 154 and numbers of eggs embryos in a brood varied from 61 to 130. These figures apply to specimens over 15 mm from anus to the base of the tentacles, and the number of eggs was related to the number of

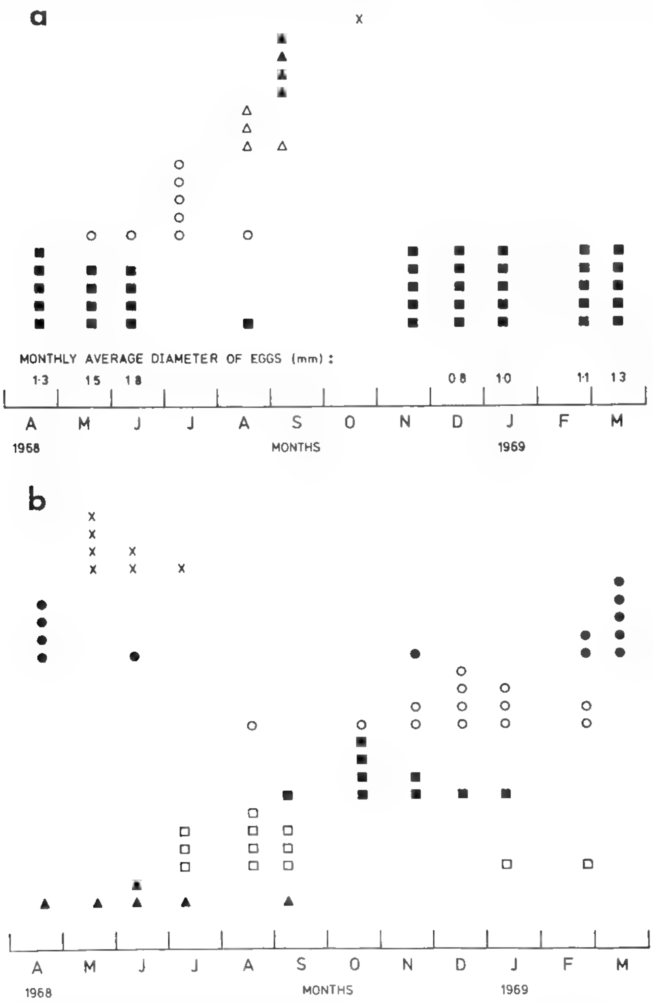

Fig. 7. Reproductive cycle of *Pseudopsolus macquariensis*. **a.** females, N = 5 each month (except October); X = no brood found in forty specimens — all juveniles released, ▲ = juveniles in brood, △ = embryos in brood, O = eggs in brood, ■ = eggs in ovary; **b.** males, N = 5 each month; X = recent spawning, ● = ripe, O = abundance of spermatids, ■ = early spermatogenesis, □ = regressed, ▲ = resorbing. (Each symbol represents one specimen (except for females in October), the gonad of which has been classified by its predominant reproductive state. The sets of each symbol are stratified on the figure for better visual interpretation.)

tubules and animal size; that is, the more tubules and/or the larger the animal, the more eggs. Eight females of 12 to 15 mm in length (in the above dimension) had egg numbers of 25 to 52 in the large caeca.

Figure 7 shows the annual reproductive cycle for *Pseudopsolus macquariensis*. Eggs were developing in the ovaries from November to June. In December, the eggs (averaging 0.8 mm diameter) were distinctly separate down the length of the caeca, resembling a string of beads. The size of the eggs progressively increased in the following months and in May, their diameter was 1.5 mm. In May and June, eggs appeared in internal brood sacs and at this stage were 1.8 mm in diameter. There was negligible variation in the size of eggs in an individual at any particular phase of the cycle. In the first week of July, all specimens assuming the female role had eggs in the internal brood sacs. There was no evidence of internal connection to these sacs. External transference was not observed nor did any specimen collected show an intermediate

phase, with some eggs in caeca and some in incubatory sacs. However, two females were found with a small stone in a brood sac that also housed eggs. This suggested insertion of eggs into the brood sacs from the outside.

Further development proceeded in the brood sacs, the September samples showing advanced embryos and juveniles. Release of juveniles occurred in late September-October. There was a high degree of synchronization during juvenile release. On 22nd October, juveniles were found underneath adults and large numbers of adults were collected on this date. Forty specimens from this collection were dissected and not one contained any juveniles.

The resting period of the testes was from July to September. Early spermatogenesis was predominant in October. Spermatogenesis and growth continued progressively with large, ripe testes predominating in March-April. In May and June, testes were in an obvious post-spawning condition, i.e. reduced, not firm, and full of mature spermatozoa with little spermatogenic activity. The cycle in the testes indicated that the breeding season occurred in May-June during the transfer period of the eggs from gonadal caeca to incubatory sacs. If the eggs are transferred externally, as findings here suggest, fertilization may depend on the coincidental timing of transfer and male spawning.

Two large, often convoluted, protuberances appeared on the ventral surface of many individuals, about half-way down the body (fig. 8). At first it was thought that these were "brood pockets" from which the young were released as the bulges coincided with the openings to the incubatory sacs. However, the protuberances were present in specimens assuming both male and female roles. The number of specimens with these growths increased during the juvenile-release phase of the cycle but with no bias to those acting as females. Histological sections of these areas showed that the extra growth was largely a result of increased connective tissue. The significance of these protuberances remains unexplained.

The incubatory sacs were deeply internal and not surface pockets. There were two sacs, divided into compartments, situated in the left and right ventral interambulacral areas. Each sac had a ventral opening via a single duct. Figure 9 shows a brood sac with eggs and a transverse section through the ventral duct. The opening was a simple hole, half-way down the ventral body wall and coinciding with the previously described protuberances (if they were present). Juveniles were released through these ventral pores and moved out from underneath the parent on to the surrounding rock surfaces. The walls of the sacs were transparent and of light texture.

Pseudocnus laevigatus (Verrill)

Only four specimens were collected from rock pools in the lower eulittoral zone. The largest individual (35 mm in length, from the base of the tentacles to the anus) contained 93 young in internal brood pouches. The brooding habit in this species has been previously reported by Pawson (1968).

Trachythyone macphersonae Pawson

Ten specimens of this species were collected from rock pools in the lower eulittoral zone. The sexes are separate. There were no small gonadal caeca opposite in sex to large caeca as in *Pseudopsolus macquariensis*. The females had a small number (110 to 130) of eggs in long, unbranched ovarian caeca; these eggs were large, diameters ranging from 0.2 to 0.8 mm with a fairly uniform size in any one specimen. The size of the egg appears to depend on the stage in the reproductive cycle. However, the small number and the 0.8 mm size eggs indicated that this species does not have a planktonic larval stage, most likely developing via a brooding habit.

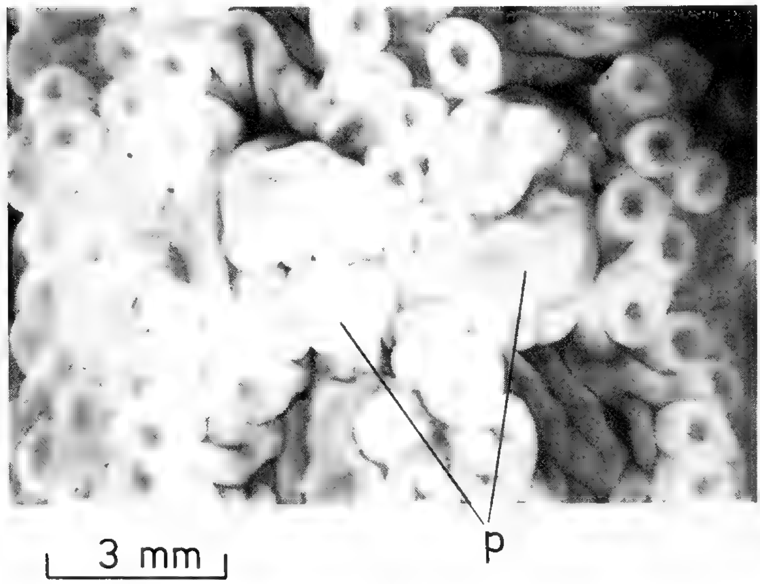

Fig. 8. Protuberances on the ventral surface of *Pseudopsolus macquariensis*, (p. = protuberances).

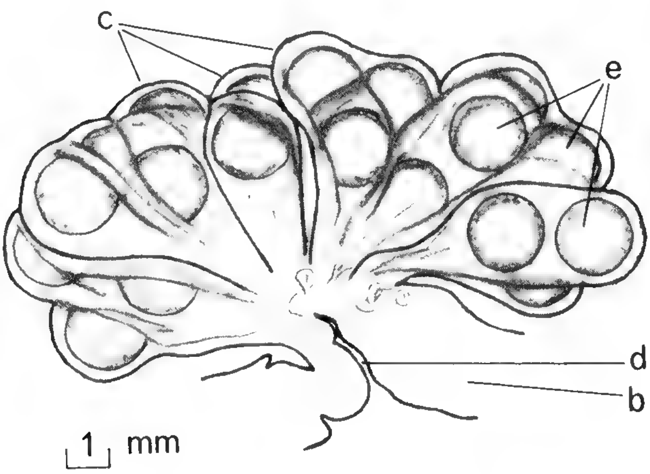

Fig. 9. Side view of brood sac and ventral duct of *Pseudopsolus macquariensis*. **b.** = ventral body wall, **c.** = compartments in the brood sac, **d.** = ventral duct, **e.** = eggs.

Pseudechinus novaezealandiae (Mortensen)

Four specimens of *P. novaezealandiae* were examined. Two were from collections during the present study (one from the sub-littoral zone, the other from a diving station at a depth of seven metres) and two were obtained from the National Museum of Victoria. As in other regular echinoids, there were five gonads suspended by mesenteries along the inner surface of the interambulacra. Three of the specimens were males, the other female. In the female, the ovaries were large and projected well down ventrally, filling a large part of the available space. The ovaries contained numerous eggs (diameter = 0.1 mm) suggesting that this echinoid has a planktonic larval stage.

DISCUSSION

For the seven species investigated, *Anasterias mawsoni*, *Anasterias directa*, *Pseudopsolus macquariensis* and *Pseudocnus laevigatus* were found to have a brooding habit. Ovarian conditions suggested non-pelagic development for *Trachythyone macphersonae* (most likely via brooding) and for *Cycethra macquariensis* (most likely via the laying of egg masses), and a pelagic larval development for *Pseudechinus novaezealandiae*. These predictions of larval development for the latter three species are based on the number and size of the ova. Invertebrate species with a non-pelagic larval development characteristically have a small number and large size of eggs (Thorson, 1950 and Mileikovsky, 1971.). The suitability of this type of prediction is discussed elsewhere (Simpson, 1977) as well as the less positive nature of the converse — that a large number of small eggs indicates a pelagic development.

For the four species collected at regular intervals, both *Anasterias* and *Pseudopsolus macquariensis* were found to have an annual reproductive cycle. *Cycethra macquariensis* appeared to breed continuously throughout the year. From the respective numbers examined, the sex ratios varied among the four species, that is female: male was approximately 1.5:1 *(Anasterias mawsoni)*, 1:1 *(Anasterias directa)*, 0.5:1 *(Cycethra macquariensis)*, and 0.8:1 *(Pseudopsolus macquariensis)*. However, no attempt was made to randomize collecting localities and hence the ratios may be affected by any sexual bias in distribution.

The reproductive condition found in *Cycethra macquariensis* is atypical for starfish. They generally have a well defined short breeding season, usually as part of an annual reproductive cycle (Boolootian, 1966). In a list of breeding seasons of asteroids compiled by Boolootian (1966), the two exceptions to this rule were in the family Asterinidae *(Patiria miniata* and *Asterina exigua)* which were reported as breeding continuously throughout the year.

Lawson-Kerr and Anderson (1978) confirmed that *Patiriella exigua* (named *Asterina exigua* by Mortensen (1921) in Boolootian's list) was potentially capable of breeding at any time of the year. A further species reported as being capable of breeding throughout the year is also in the family Asterinidae — *Patiriella vivipara* (Dartnall, 1969).

Although some species of asterinid starfish have limited breeding seasons, (Boolootian, 1966; Lawson-Kerr and Anderson, 1978; Komatsu, pers. comm.), it is curious that all starfish reported as capable of continuous breeding are in the Asterinidae. To elucidate the reasons for the reproductive strategies of marine invertebrates, many factors require examination. One of these factors is phylogenetic affinity for a particular reproductive type. It would seem that asterinid starfish present appropriate material for investigating such a factor.

Anasterias mawsoni and *Anasterias directa* had the same distributional range, occupied similar habitats and had very similar prey (Simpson, 1976b); yet their reproductive cycles were different in that there was a time difference of four months between the peak release of young

nd hence recruitment of the two species. This may be important in alleviating any competition etween the recruitment of the two species into such similar ecological niches.

For the species collected, there is a predominance of a protective mode of larval levelopment with a comparatively small number of offspring. This conforms with "Thorson's ule" that there is an increase in frequency of non-pelagic development with increasing latitude. The adaptive significance of this phenomenon has been the subject of much speculation and nany hypotheses, which are linked to changing physical and biotic ecological conditions with ncreasing latitude (Thorson, 1950; Mileikovsky, 1971; Menge, 1975).

The sub-Antarctic provides an important link in records of reproduction of marine nvertebrates from tropical and temperate regions to the Antarctic. Gathering of data on the node of reproduction of invertebrates from selected groups across the range of southern atitudes should result in better interpretation of zoogeographical origins and lines of listribution. This will provide a more complete historical background to possible investigations of adaptational advantages to be gained by animals with a protective mode of development in igher latitudes. Details of the timing of the events, when reproductive patterns of such animals an be obtained, will allow insight into key areas for such investigations.

ACKNOWLEDGEMENTS

I should like to thank Ms. I. Bennett for her advice on the known life histories of chinoderm species at Macquarie Island prior to the expedition. Mr S. Harris greatly assisted in collecting specimens. The collections were made possible by the support of the Antarctic Division, Department of Science, Australian Government. I am indebted to Professor J. S. Pearse for helpful comments on some of the data.

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4. SEXUAL AND ASEXUAL REPRODUCTION OF *HOLOTHURIA ATRA* JAEGER AT HERON ISLAND REEF, GREAT BARRIER REEF

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SUMMARY

H. atra is the most common epifaunal holothurian on the reef flat at Heron Island. The gonad maturation cycle of *H. atra* was followed using gonad index estimations and histological examination. Gonad samples were taken at intervals of 6 to 8 weeks for 18 months. Mature gonads occurred in most samples, and gonad maturity peaked twice; in early winter and in summer. Sex ratio of female to male animals was not significantly different from a 1:2 ratio. Sex ratio ranged from 1:8.5 in animals weighing less than 100 g, to 1:0.7 in those over 1,000 g. *H. atra* commonly reproduces asexually by transverse binary fission. In 21 samples, each of approximately 50 animals, 6% to 70% of individuals were detectable products of asexual reproduction. Occurrence of frequent asexual reproduction compounds difficulties in estimation of growth parameters from data such as size-frequency distributions and growth increments.

INTRODUCTION

Holothurians are amongst the most common coral reef macro-invertebrates, but little information is available on their reproductive biology (Bakus, 1973). An understanding of reef systems requires data on the population dynamics and patterns of recruitment of these, and many other reef species.

Temperate holothurians, in common with other temperate marine invertebrates, generally spawn for a limited period during spring or summer (Boolootian, 1966). Tropical species, however, exhibit a variety of spawning patterns. Holothurians are also known to reproduce asexually, by transverse binary fission (Hyman, 1955; Bonham and Held, 1963).

Holothuria atra Jaeger is widely distributed in the Indo-West Pacific region, and is the most common epifaunal holothurian on the reef flat at Heron Island. In this habitat, it is generally found on sandy substrata.

Pearse (1968) studied sexual reproduction of *H. atra* at several low latitude sites in the tropical Indo-Pacific. Because individuals with mature gonads were found throughout the year, he concluded that spawning was asynchronous. He predicted that populations distant from the equator would have more restricted spawning periods.

Bonham and Held (1963) reported asexual reproduction by fission in *H. atra* at Rongelap Atoll, Marshall Islands, and suggested that fission occurred commonly. Ebert (1978) interpreted the apparently high rate of asexual reproduction in *H. atra* at Enewetak Atoll, as an adaptation enabling the species to span periods of unsuccessful recruitment from the sexual phase.

The relative frequency of recruitment from sexual and asexual modes of reproduction is a potentially important life history parameter. This paper reports on sexual and asexual reproduction in *H. atra* at different sites on Heron Island reef, in the Capricorn Group, at the southern extremity of the Great Barrier Reef (Lat. 23° 27′ S).

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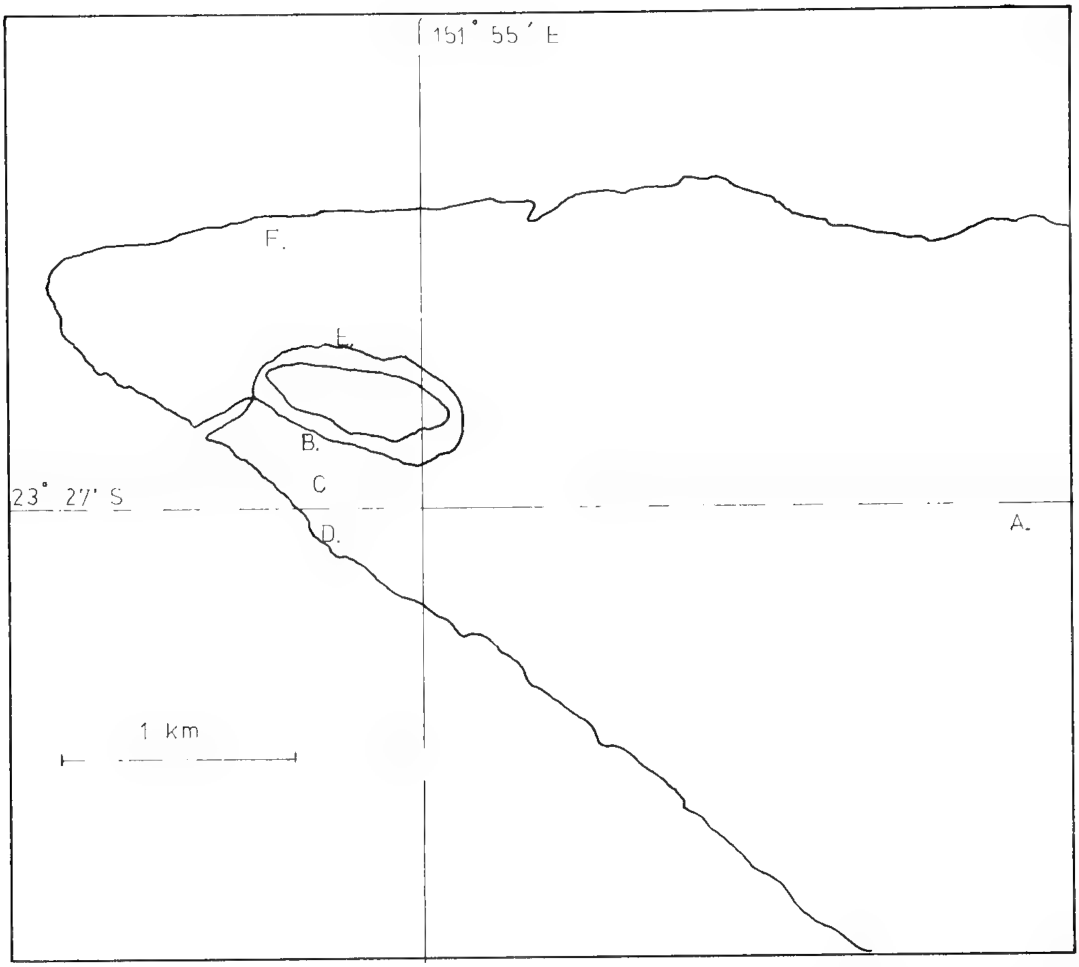

Fig. 1. Heron Island reef showing sample sites. A = shallow lagoon; B = S. W. reef flat, gutter; C = S. W. reef flat, mid-reef; D = S. W. reef flat, crest; E = N. E. reef flat, inshore; F = N. E. reef flat, rubble crest.

METHODS

Sites sampled on Heron Reef during the course of the study are shown in Figure 1.

1. SEXUAL REPRODUCTION

The reproduction cycle of *H. atra* was studied over 18 months, from December, 1976 to June, 1978. Gonads were sampled at intervals of 6 to 8 weeks during this period. Sexual reproducton was studied in 2 ways; (a) by use of gonad index estimation, and (b) by histological examination of excised gonads.

(a) Gonad index estimation. For each sample, individuals of *H. atra* were collected from the lagoon of Heron Island reef (fig. 1; site A). Sample size ranged from 12 to 24, with a mean sample size of 16 individuals. The animals were taken to the laboratory and maintained overnight in aerated aquaria to allow emptying of the guts. Wet weight of the animals was measured to the nearest 5 g, and gonads were exised and weighed to the nearest 0.01 g. The gonad index was calculated as the ratio of wet gonad weight to wet body weight, expressed as a percentage, for each individual. The mean gonad index ($\pm$ S.E.) was calculated for each of the 13 samples obtained.

(b) Histology of gonads. Excised gonads were preserved and fixed in alcoholic Bouin's fixative and stored in 70% ethyl alcohol. They were dehydrated, cleared, embedded in paraffin wax, and sectioned at a nominal thickness of 10 μm Sections were stained with haematoxylin and eosin.

Gonads were assigned to one of three classes of maturation, derived from those recognised by Tanaka (1958) —

(i) Resting stage and indeterminate gonads.
(ii) Recovery stage and growing stage gonads.
(iii) Mature stage and shedding stage gonads.

The sex ratio was recorded for individuals of a wide range of weights. These animals were collected from several habitats.

2. ASEXUAL REPRODUCTION

Samples of 33 to 100 individuals, each weighing less than 90 g, were collected from 6 habitats, A to F (fig. 1). Habitats A, B and C were sampled five times (between August, 1977 and June, 1978), habitat D was sampled four times, and habitats E and F were sampled once only. Each individual was dissected and examined for the following signs of recent binary fission, as recognised by Crozier (1917).

a. An abnormally large or small calcareous ring.
b. A change in colour or texture of the internal body wall at the region of regeneration.
c. The absence or smallness of either anterior or posterior body organs.
d. A narrowing of the five longitudinal muscle bands at the line of division.

For each fissioned individual, the degree of regeneration following fission was determined, and scored on a scale of 0-3 by the following criteria —

0. No visible regeneration; very recent division.
1. First signs of regeneration of gut, mouth or anus; very small calcareous ring present (less than 5 mm diameter); body wall regrowth less than 1 cm in length.
2. Body organs regenerated but small; body wall regrowth 1-3 cm.
3. Complete regeneration of body organs; discernable as fission product by narrowing of muscle bands and difference in colour of body wall; body wall regrowth over 3 cm.

The percentages of fissioned individuals in early stages of regeneration (stages 0 and 1) were plotted against time to indicate changes in the frequency of recent division.

3. POPULATION SIZE STRUCTURE

Size-frequency distributions were used to ascertain population size structure in the habitats from which specimens had been examined for asexual reproduction. Samples of 80-300 individuals were weighed in the field to ± 5 g, and weights plotted to produce size-frequency histograms.

RESULTS

1. SEXUAL REPRODUCTION

From Figure 2, the plot of gonad index over time, seasonal variations in gonad index are apparent. Gonad index peaked at 1.8%, 2.7% and 1.2% in May, 1977, December, 1977 and May, 1978 respectively. Each peak was followed by a decrease in gonad index to 0.3% and 0.8% and 0.4% respectively, indicating possible spawnings during the months of May/June and December/January.

Seasonal changes in histological state of the gonads are recorded in Figure 3. Changes in percentages of mature gonads closely parallel changes in gonad index, indicating that, for this species, gonad index is a good measure of gonad maturity. The percentage of mature gonads peaked at 75% and 100% in May and December, 1977 respectively.

Histological data confirm that spawning follows these peaks in gonad maturity. A decrease in the percentage of mature gonads is accompanied by an increase in the percentage of histologically determined spawned gonads.

Spawning occurred later in summer 1977-78 than it did the previous year, when individuals had spawned by mid-December.

Differences in reproductive cycle between male and female individuals were indeterminable because of the small numbers of females in some samples (Table 1).

Hermaphroditic gonads, that is, those containing both male and female gonad elements, were detected in 2 of the 155 individuals examined.

Sex-ratio for individuals of *H. atra* from different samples is shown in Table 1. The sex ratios were tested for homogeneity using a X^2 test, and were found to be sufficiently homogeneous to permit pooling ($p > 0.05$). Pooled data were tested, and the ratio was found to differ significantly from 1:1 ($X^2 = 24.25$, $p < 0.01$), but was not sifnificantly different from a 1:2 ratio of females to males ($X^2 = 0.04$, $p > 0.5$).

Figure 4 shows the relationship between sex and size (weight), for all individuals examined. Because of small sample size, results have been pooled for the large size classes. The relationship between sex and weight was tested using X^2 contingency table analysis, and sex was found to be dependent on size class ($p < 0.02$). In individuals weighing less than 100 g for which gonads are recorded, the ratio of females to males was 1:8.5 ($n = 21$); while in those individuals over 1,000 g, the ratio was 1:0.7 ($n = 11$).

2. ASEXUAL REPRODUCTION

Table 2 shows the percentages of detectable products of asexual reproduction in each sample, from the habitats indicated. Small individuals, i.e. those less than 100 g were sampled because fission products will eventually regenerate and become unrecognisable. Fission

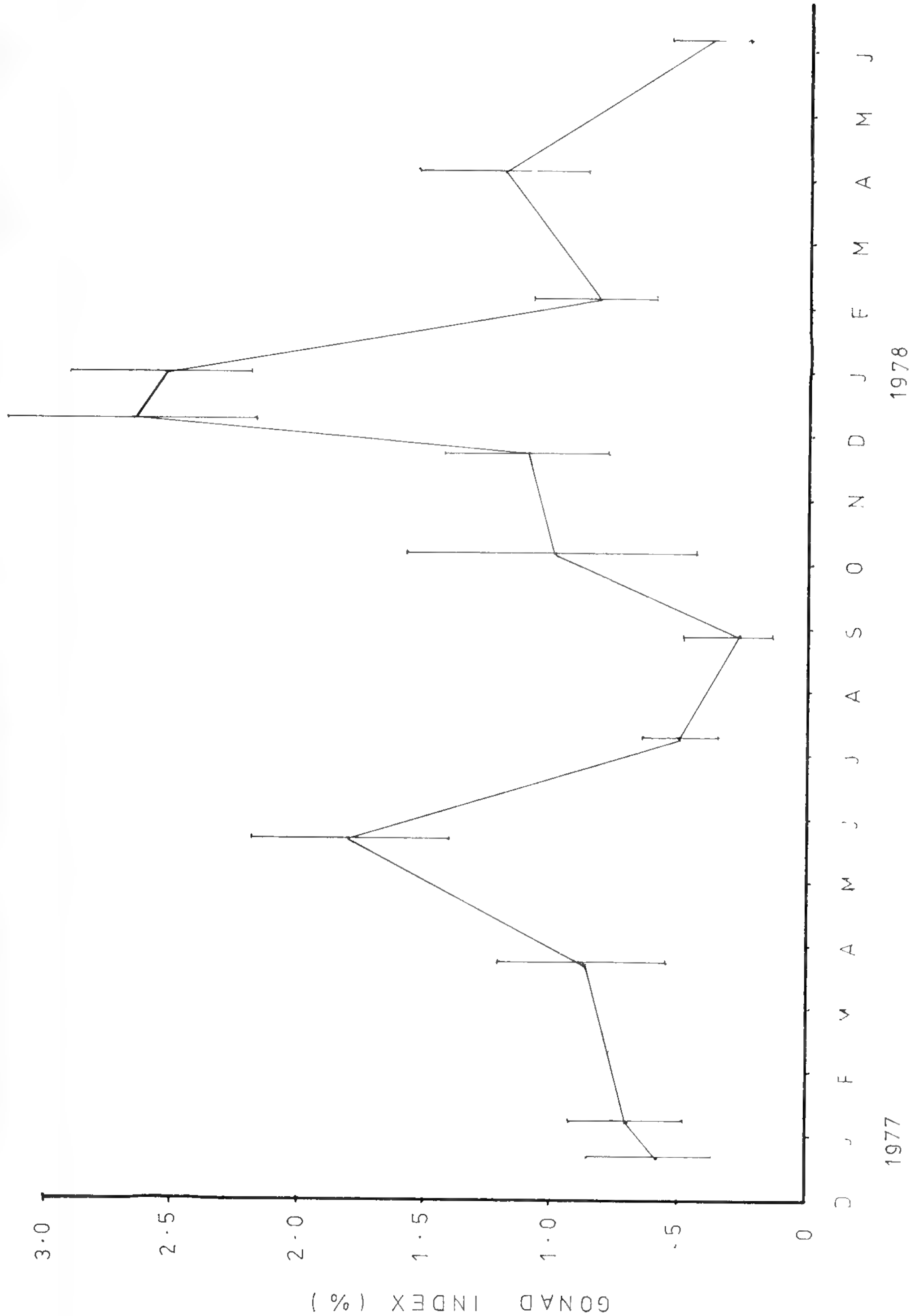

Fig. 2. Seasonal changes in mean gonad index of *H. atra* (December 1976-June 1978). Vertical lines show range of standard error.

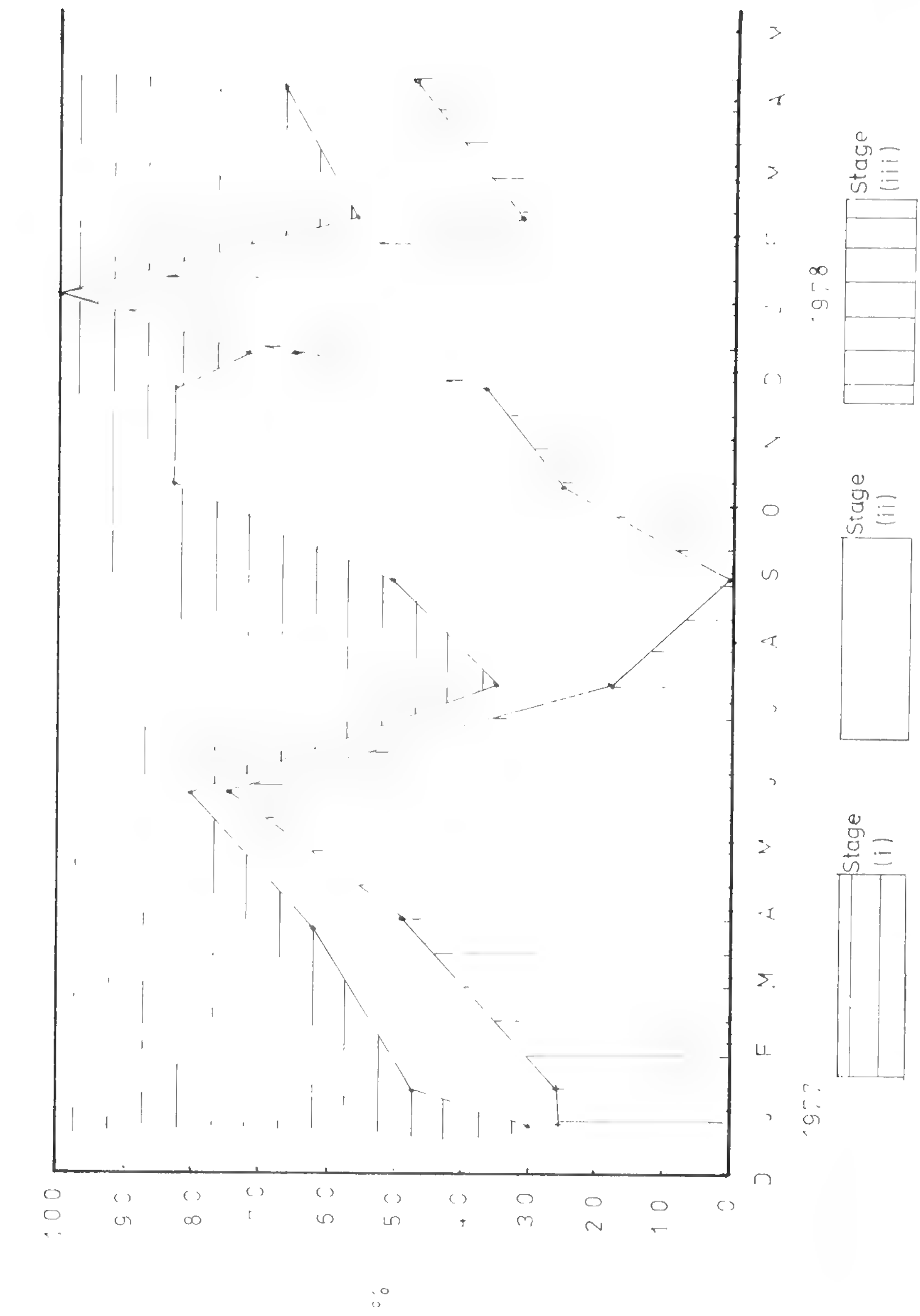

Fig. 3. Seasonal changes in gonad maturation of *H. atra* (December 1976 - April 1978), showing the percentages of individuals of each sample which were in the stages (i) Resting stage and indeterminate, (ii) Recovery and growing stage, (iii) Mature and shedding stage.

TABLE 1. Abundance of male and female *H. atra*, sampled from lagoon, unless specified.

	♀	♂
December 1976	6	3
January 1977	4	10
March, 1977	2	9
May, 1977	6	10
July, 1977	3	6
August, 1977	4	7
October, 1977	0	8
October, 1977 — Crest	6	4
November, 1977	5	16
November, 1977 — Flat	4	6
November, 1977 — Gutter	5	14
December, 1977	5	8
January, 1978	4	12
January, 1978 — Crest	4	4
February, 1978	5	10
April, 1978	4	9
n = 202	66	136

products were rarely detected in the individuals greater than 100 g that were sampled for gonads.

Differences in frequency of fission among these samples were tested using X^2 contingency table analysis, at the 95% confidence level. Several patterns are apparent from the data, e.g.:

a. The frequency of asexual reproduction is significantly dependent on habitat for all months, with $p(X^2) < 0.001$, except in February 1978 when $p(X^2) = 0.006$.
b. In the lagoon and reef crest, the percentage of fission products is dependent on time $p(X^2) > 0.005$).

Figure 5 shows changes in the percentage of recent divisions (stage 0 and 1), over the period sampled, in the gutter habitat (fig. 1, site B). Division is more frequent in the period preceding August 1977 than in the period preceding June 1978. This result is supported by the changes in fission frequency with time in some habitats, and suggests that fission frequency is not constant throughout the year, but is maximal during limited periods.

The ratio of former posterior to former anterior ends was approximately 1:1, indicating a similar mortality rate for each section.

Fission rate appears to be approximately equal in males and females, although only a small percentage of fissioned individuals examined contained detectable gonads. Of the 38 individuals with visible gonads, 12 were female, 15 were male, and 11 were indeterminate. Although no detailed histological examination was made, gonads examined appeared to include all stages of gonad maturity.

3. POPULATION SIZE STRUCTURE

The size-frequency distributions obtained were variable over time and habitat, but frequently conformed with one of two general patterns, unimodal or bimodal (fig. 6). No consistent age-class groups were detectable. Samples from the inshore gutter area always had a

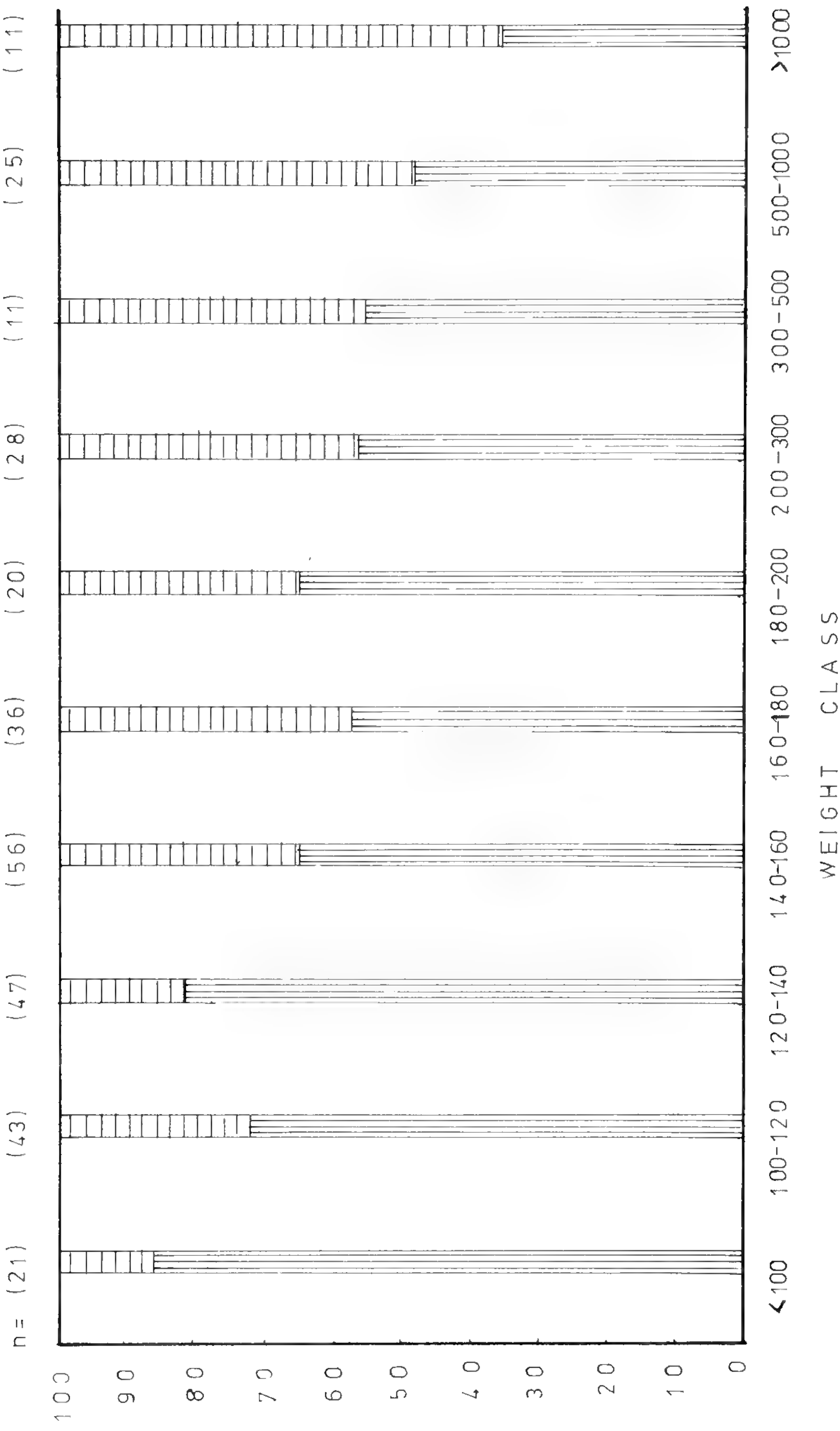

Fig. 4. Graph of changes in sex ratio with increasing weight. The ordinate represents the percentage of each weight class that was male (vertical stripes), and female (horizontal stripes).

TABLE 2. Percentages of *H. atra* samples (sample numbers in brackets) that were discernable products of asexual reproduction in 6 habitats of Heron Island reef from August 1977 to June 1978.

HABITAT	August 1977	October 1977	Nov./Dec. 1977	February 1978	April 1978	June 1978
S. W. Reef Flat						
Gutter	61% (51)		58% (56)	58% (52)	56% (50)	51% (50)
Crest	11% (44)		22% (58)	37% (48)	22% (50)	6% (50)
Mid-Reef	40% (33)			62% (51)	60% (45)	70% (46)
Lagoon		20% (65)	14% (50)	34% (50)	52% (50)	52% (52)
N.W. Reef Flat						
Rubble crest		47% (108)				
Inshore			50% (50)			

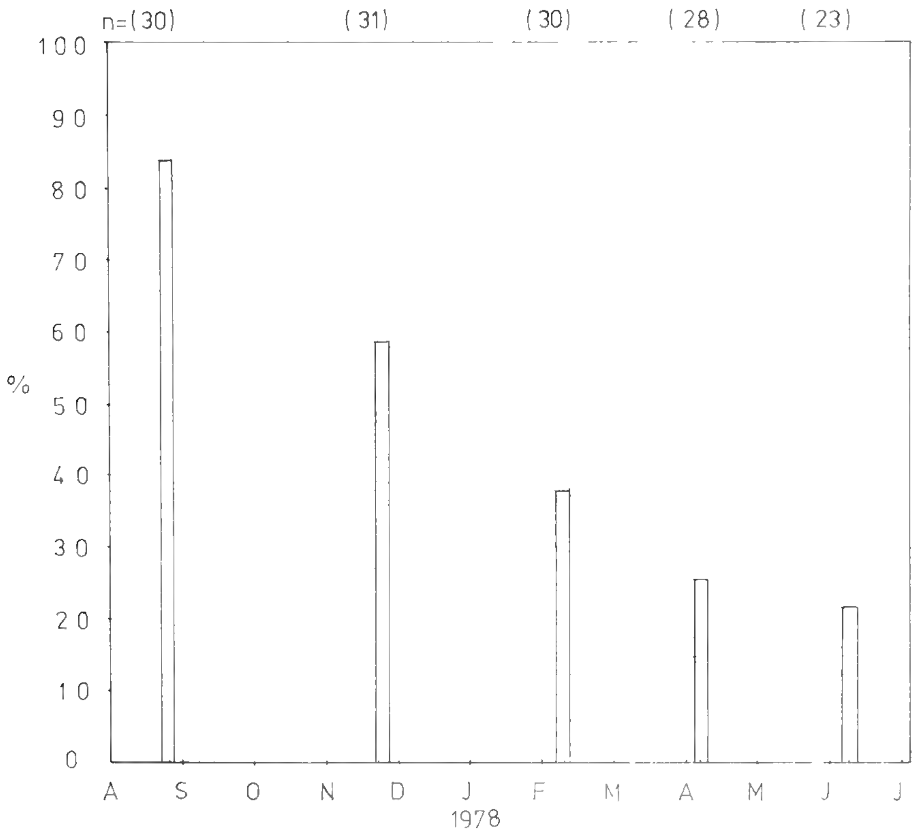

Fig. 5. Graph of percentage of fissioned individuals that were in early stages of regeneration i.e. stages 0 and 1, sampled from the S. W. reef flat gutter, from August 1977 to June 1978.

bimodal distribution, those from the reef-crest had a unimodal distribution, and samples from the lagoon and mid-reef had distributions that varied with time.

DISCUSSION

H. atra has a semi-annual reproductive cycle at Heron Island reef, and a large proportion of the population breeds in both winter and summer.

Until 1966, there was no record of semi-annual reproductive cycles in holothurians (Boolootian, 1966). Since then 2 species have been reported with this breeding pattern. *H. scabra* Jaeger in India spawns predominantly semi-annually, in summer and autumn (Krishnaswamy and Krishnan, 1967). The authors suggest that salinity changes, caused by fresh water influxes following monsoons, may induce spawning in *H. scabra* and other tropical marine animals. There are no comparable semi-annual salinity changes at Heron Island reef.

More recently, a temperate hermaphroditic species, *Leptosynapta tenuis* (Ayres), has been reported to have a semi-annual reproductive cycle (Green, 1978). The population spawned in the spring and in the fall, with a mid-summer cessation of reproductive activity. Green suggested that external factors, possibly temperature, might regulate the reproductive cycle.

A semi-annual reproductive cycle is well-known amongst other tropical marine invertebrates. The Great Barrier Reef Expedition reported a semi-annual spawning cycle (spring and autumn) in the echinoid *Tripneustes gratilla* (Linnaeus) (Stephenson, 1934). Both *T. gratilla* and *T. ventricosus* (Lamarck) vary in reproductive cycle with geographic location, but exhibit a tendency for semi-annual reproduction, and in some locations spawn in winter and summer (Pearse, 1974).

In his study of reproduction in tropical *H. atra*, Pearse (1968) found that spawning was asynchronous, mature gonads being present throughout the year. He suggested that breeding season would become more restricted with distance from the equator. This proposition is supported by the present study, since mature gonads were found in almost every sample, but the majority of individuals spawned in two limited periods.

The semi-annual reproductive cycle of *H. atra* is not typical of other species of holothurians studied at Heron Island reef. *H. impatiens* (Forskaal) (unpub. data) and *H. leucospilota* (Brandt) (S. Franklin, pers. comm.) are both synchronized annual breeders, spawning in spring or summer. Spawning in *H. edulis* (Lesson) is apparently non-synchronized and non-cyclic (unpub. data).

Several hypotheses may be proposed to account for the change in sex ratio of *H. atra* with increased size. Three hypotheses are presented here.

a. Mortality rates of male and female animals may change throughout their life-span. Mortality rate may be high in female individuals before sexual maturity, and in male individuals after sexual maturity. It is difficult to postulate biotic or abiotic factors that might contribute to this differential mortality.

b. A relatively higher rate of fission in male individuals than in females would lead to a higher incidence of males than females among small animals and a higher incidence of females than males among large animals. However, available data on sex of fission products (15 male, 12 female, 11 indeterminate) suggest that the sex ratio of fission products is approximately 1:1. Because of the small number of fission products for which sex data are available, this theory cannot be entirely discounted.

c. Some proportion of the population of *H. atra* may exhibit protandrous

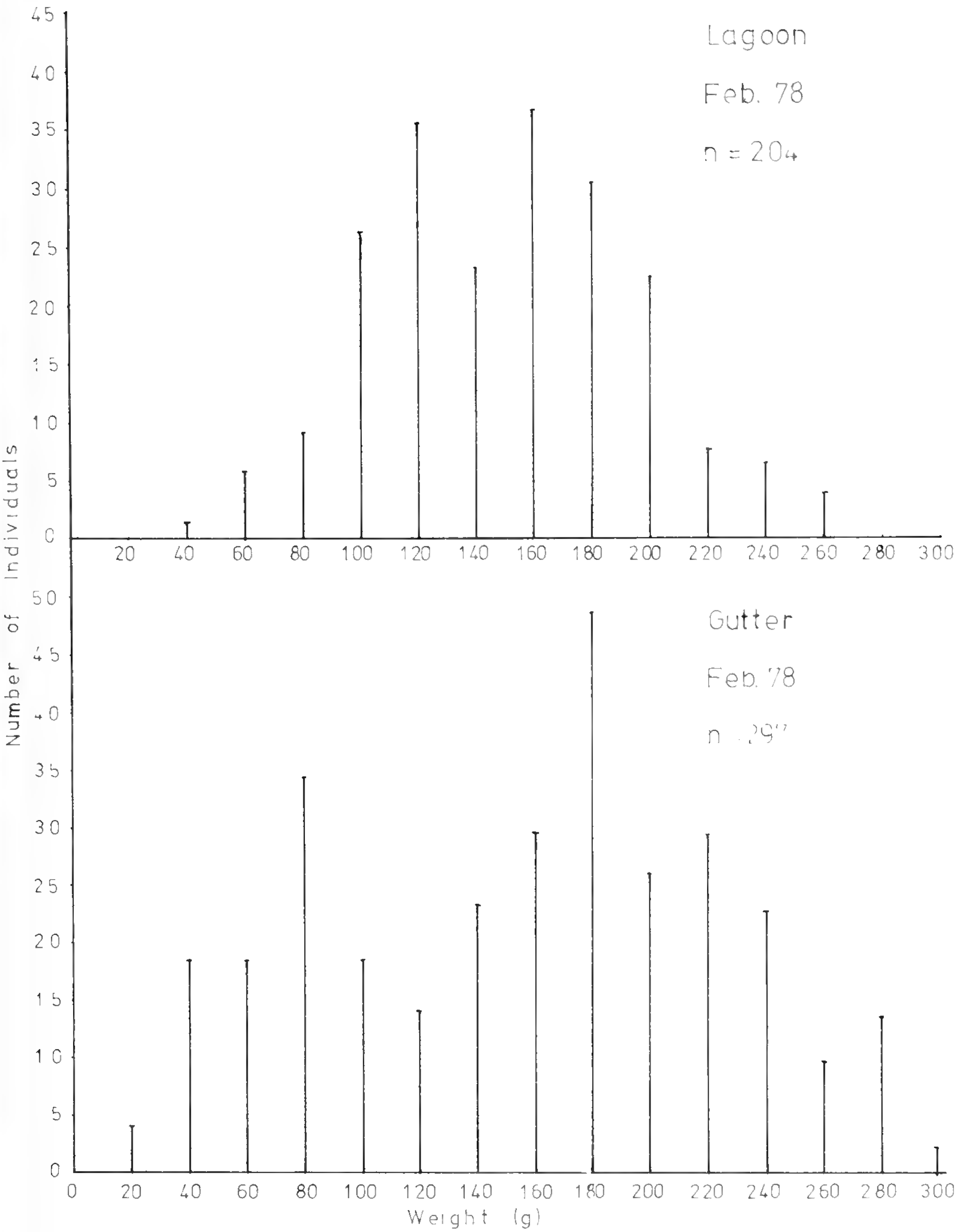

Fig. 6. Typical size-frequency distribution patterns of *H. atra;* unimodal (lagoon) and bimodal (gutter).

hermaphroditism. Hermaphroditism is common in holothurians and otl echinoderms (Hyman, 1955), and protandrous hermaphroditism has been recorded several echinoderms (Bacci, 1965). At some stage during their growth, a cert proportion of individuals may change from males to females. This hypothesis is diffic to test as gonads regress after each spawning, and may disappear before the developm of new gonads. It is impossible to determine the sex of previous gonads. T hermaphroditic gonads have been detected amongst those sectioned to determine reproductive cycle. It is possible that individuals may change sex more than once duri their lifetime.

Although transverse fission in holothurians is a commonly recorded phenomenon (Hyma 1955; Bonham and Held, 1963), few studies include any quantitative data on the importance asexual reproduction in the life-histories of the species. Crozier (1917) found evidence of bina fission in 11% of individuals of *H. surinamensis* Ludwig examined, and concluded that fissi represented a regular means of multiplication in the species. Deichmann (1922) found 50 regenerating specimens of *H. difficilis* Semper, and 65% of *H. parvula* (Selenka), in samp studied. The mode of division in these species is apparently identical with that of *H. atr* Fissioned and fissioning specimens of *Stichopus horrens* Selenka, *S. chloronotus* Brandt and *edulis* have been found by the author at Heron Reef, the latter commonly.

The frequency of asexual reproduction is related to habitat. In general at any one tim fission frequency is greater in the gutter and mid-reef habitats than in the S.W. reef-crest a lagoon habitats. From the present study, it is impossible to distinguish causative factors in t relationships between habitat and frequency of asexual reproduction. Pearse (1968) suggest that fission may be more frequent in *H. atra* in surf-swept intertidal areas. This is supported b the low fission frequency of the lagoon, but contradicted by the unusually low rate for the S.W reef-crest.

It is probable that many factors contribute to the variation in fission rate with habitat, an these may include temperature, exposure, current flow, food availability, or more comple factors such as "patchiness" of resource distribution within a habitat, or possible genet differences between populations. The latter would depend on a limited flow of genetic materi between populations, and may not be compatible with the existence of free-livin planktotrophic larvae of *H. atra*.

Ebert (1978) suggested that asexual reproduction accounts for the absence of large *H. atr* on the reef flat at Enewetak Atoll, and that fission is promoted by environmental factors. H interpreted the high rate of asexual reproduction in *H. atra* as an adaptation to the lo recruitment rate from the sexual phase. *H. atra* is common at both Enewetak Atoll and Hero Island, and the high frequency of asexual reproduction may contribute to its abundance.

Data on changes in frequency of asexual reproduction over time in some habitats, and dat on changes in regeneration states over time, indicate that fission is more frequent during limite periods of the year. Whether this change in frequency follows a yearly cycle cannot b determined from the data available.

Bonham and Held (1963) suggested that sexual reproduction may be seasonal, whil asexual reproduction by binary fission could occur throughout the year. This study shows tha both sexual and asexual reproduction may occur at low frequencies throughout the year, bu with highest frequency of each during one or more limited periods.

Size-frequency distributions can be correlated with frequency of asexual reproduction. In areas of high fission frequency, samples were generally bimodally distributed, and in areas of low fission frequency, a unimodal distribution was most common. The lower peak of the

bimodal distributions were composed of individuals weighing less than 90 g, and a large proportion of these were products of asexual reproduction. Absence of age classes in the size-frequency distributions could be related to the relative importance of recruitment of fission products to the population.

In some organisms, growth has been estimated by obtaining growth increment data from tagged individuals, and applying growth equations such as the Brody-Bertalanffy equation. This method has been successfully applied to echinoids (Ebert, 1977) using tetracycline tagged skeletal elements, and has been tested on holothurians (Ebert, 1978). These analyses of growth are complicated when individuals undergo asexual reproduction. Calcification rates, used as an estimator of growth, may not be uniform in former oral and former anal ends. The size of the calcareous plates will have no relationship with the overall size of the animals, so most growth equations become inapplicable. If individuals divide more than once in their lifetime, mortality may be impossible to define or measure.

Overall, the unusual growth and reproductive characteristics of this species indicate that traditional growth analyses have little value in obtaining meaningful data on growth and mortality.

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5. A NEW GENUS AND SPECIES OF OPHIACANTHID BRITTLESTAR (ECHINODERMATA: OPHIUROIDEA) FROM THE KERGUELEN ISLANDS, WITH NEW TAXONOMIC, BIOGEOGRAPHIC AND QUANTITATIVE DATA ON THE ECHINODERM FAUNA

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SUMMARY

Forty-two species have been sampled on the continental shelf of Kerguelen islands during MD04/Benthos cruise of M.S. "Marion-Dufresne" (March 1975). Among the species, the taxonomic position of a few animals is still uncertain. Four ophiuroids however, allow interesting taxonomic and biogeographical comments: a new genus and new species in the family Ophiacanthidae, *Ophioparva blochi*, is described; *Ophiomisidium speciosum* Koehler was known previously only from the tropical deep Atlantic; *Ophiocten hastatum* Lyman and *Ophiocten amitinum* Lyman are placed in the genus *Ophiura*. The fauna has a generally wide antarctic and sub-antarctic distribution, but a few species are endemic to the Kerguelen province. *Ophiura hastata* and the newly recorded *Ophiomisidium speciosum* are also known from the deeper parts of the sub-tropical Atlantic.

On the continental shelf, the average density of echinoderm individuals is 52.8 m^2 at depths between 10 and 180 metres. In fjords, the density of individuals is high but the number of species is low. On the contrary, outside of the fjords in open sea, the density of individuals is low but the specific diversity is high. Around the Kerguelen islands, the specific and quantitative composition of the echinoderm fauna is correlated with hydrological conditions, in particular with the west wind drift.

INTRODUCTION

The Kerguelen islands are located approximately 50°S latitude, 70°E longitude, at the limit of the antarctic convergence, in the southern part of the Indian Ocean, half-way between South Africa and Australia. The bionomic and physiographic characteristics of the continental shelf of the archipelago, as well as the fjords and interior gulfs and bays, have been the subject of several publications (Desbruyeres and Guille, 1973 and 1977; Guille and Soyer, 1976; Guille, 1977a and b; Murail, David and Panouse, 1977).

Since 1972, an intensive programme of bionomic and biological research has been in operation on the benthic fauna of the continental shelf of the Kerguelen islands, in particular on the echinoderms. After the study of the qualitative and quantitative composition of the echinoderm fauna of the Morbihan gulf, virtually an enclosed sea with distinct hydrological and substrate conditions (Guille, 1977a), a similar study has been carried out on the open sea, on the continental shelf surrounding the archipelago, during the MD04/Benthos cruise of "Marion-Dufresne" (Guille, 1977b). Before the present programme, the echinoderm fauna of Kerguelen was essentially known through the major expeditions at the turn of the century and shore collections by Rallier du Baty published by Koehler (1917). More recent studies have encompassed a wider geographic area and added to our taxonomical understanding of related faunas, Hertz (1927), Mortensen (1936), Madsen (1955), and A. M. Clark (1962). The only ecological data, pertaining to the Kerguelen echinoderms, has been given by Arnaud (1974) and Cherbonnier and Guille (1974).

The collection studied here concerns only the samples of the MD04/Benthos cruise taken by an Okean grab with a 0.5 m^2 opening. In fact, of the many kinds of benthic samplers used in

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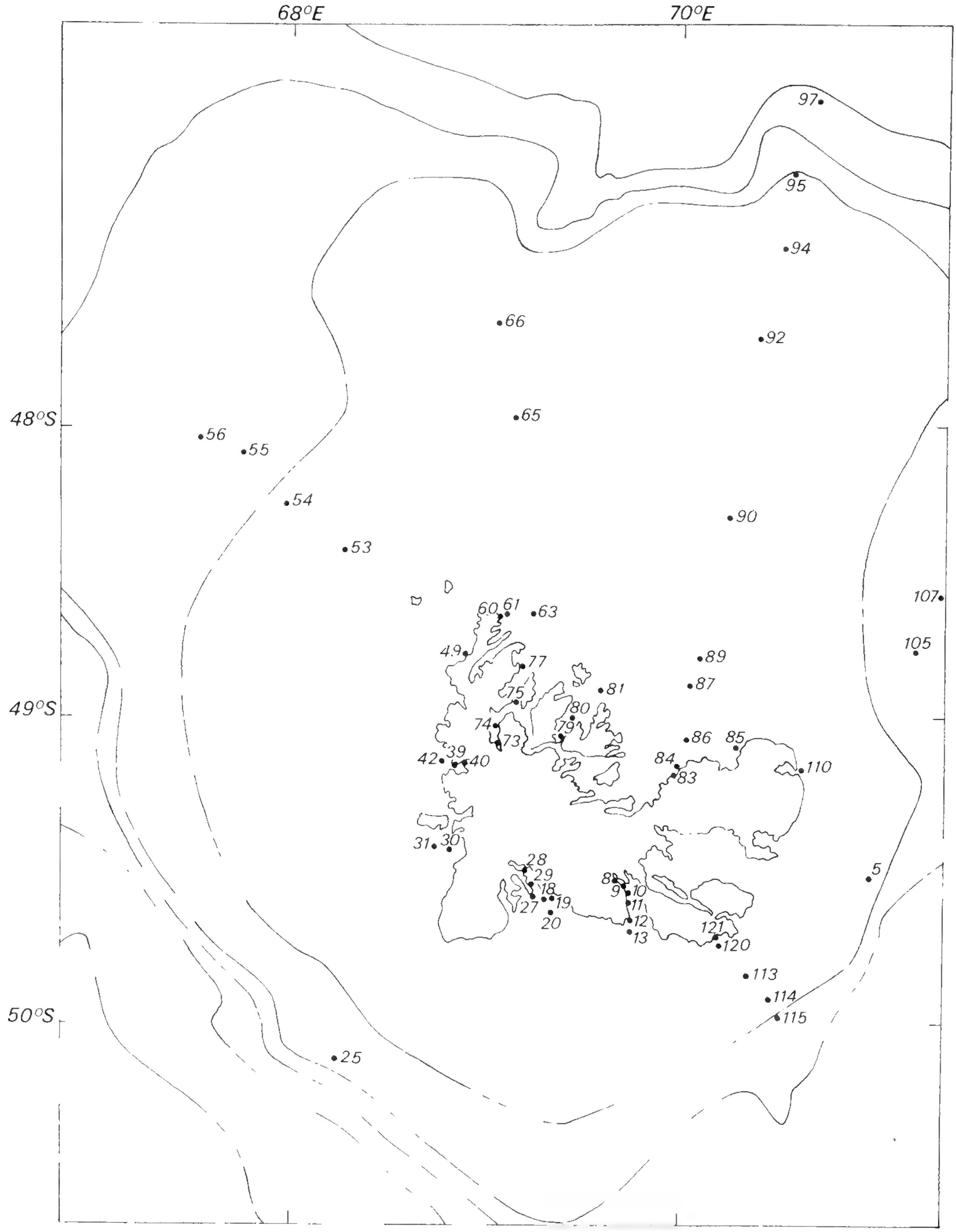

Fig. 1. Map of grab samples of MD04/Benthos cruise.

this expedition (grabs, trawls, dredges, large diameter corer), only the grabs provided a precise quantitative estimate of the fauna present. Because of the great extent of hard substrates (rock platforms and basalt pebbles), especially in the south-east region of the archipelago, the grabs were used at only 63 of the 120 stations. Of these 63 stations (fig. 1) only 45 yielded echinoderms; 34 were at depths of 10-180 metres, 8 at 180-390 metres, and 3 on the continental slope, between 843 and 1390 metres deep (cf Guille, 1977b, for geographic co-ordinates, depth, nature of substrate of each station).

SYSTEMATIC ACCOUNT

Among the 42 species collected (Tables 1 and 2; fig. 1), four species require taxonomic discussion: the discovery of the new species and genus of ophiacanthid, *Ophioparva blochi;* the species *Ophiomisidium speciosum* Koehler, previously known only from the deep tropical Atlantic; and the change of generic position of the species *Ophiura hastata* and *Ophiura amitina*, previously placed in the genus *Ophiocten*.

Family OPHIACANTHIDAE

Ophioparva n. gen.

DESCRIPTION: Disc covered entirely by small well-calcified plates, imbricated, finely granular but naked, among which are visible, only dorsally, small, widely separated radial shields, at the edge of the disc. Oral papillae contiguous, the distal one enlarged, completely closing the buccal orifice; one unpaired infradental papilla; a row of dental papillae. Genital slits elongated and narrow. Arm length up to six times the disc diameter. Arm spines erect, cylindrical. A small tentacle scale.

TYPE SPECIES: **O. blochi** n. sp.

Ophioparva blochi n. sp.

Figs 2 and 3a, b

MATERIAL EXAMINED: 13 specimens (d.d. 2.5-5.5 mm), st.5, February 22nd, 1975, 49°30.0'S-70° 56.0'E, 147 m basalt pebbles and shelly sand (holotype d.d. 5.5 mm) coll. MNHN n° ECOS 20371 and 12 paratypes (d.d. 2.5-5.0 mm) coll. MNHN n° ECOS 20371, 4 specimens (d.d. 3-4 mm), Kerguelen, st. 54, March 3rd, 1975, 48°19.0'S-67°56.5'E, 192 m, basalt gravel and muddy sand. All type and non-type material deposited in the Muséum National d'Histoire Naturelle, Paris.

DESCRIPTION: The disc diameter of the holotype measures 5.5 mm; the arms, broken, measure at least six times the disc diameter. The disc is completely calcified, pentagonal, the interradial edges straight or more or less excavated. The disc plates and the arms all have a finely granular appearance.

The dorsal side of the disc is swollen, covered with small imbricated plates, rounded or oval, among which neither the centrodorsal nor primary plates are apparent. The radial shields are at the edge of the disc, encasing the arm base, and are widely separated by several rows of plates which extend onto the first arm segments. The radial shields are small, three times longer than wide, more or less triangular, approximately equal to the one third of the disc radius (figs. 2a and 3a).

The ventral interradial areas are covered with plates similar to, but larger than, those of the dorsal face of the disc. The genital slits, mostly very narrow, are usually bordered by two or three elongated plates with either fine granules or traces of them. The oral shields are cordate, as long as broad, the distal edge broadly convex, the proximal angle subacute. The adoral shields are large, trapezoidal, more than twice as long as broad, the proximal edge shorter than the distal

Table 1. List of species with station number and specimen number ( ).

Species	Station number and number (in parenthesis) of specimens
Crinoidea:	
Promachochrinus kerguelensis P. H. Carpenter	5(4); 8(1); 9(1); 18(1); 19(1); 53(2); 54(1).
Echinoidea:	
Ctenocidaris nutrix (W. Thomson)	5(5); 113(1); 114(1).
Sterechinus diadema (Studer)	5(1); 8(3); 62(1); 75(1); 77(1); 84(1); 90(1); 113(1); 114(1).
Abatus cordatus (Verrill)	8(8); 10(1); 12(2); 18(4); 19(1); 30(3); 31(2); 49(2); 60(11); 73(15); 74(5); 79(2); 86(5); 90(1); 110(16); 113(1); 121(8).
Brisaster kerguelenensis H. L. Clark	77(1); 89(1); 92(2); 94(1); 97(1); 105(1); 107(1).
Asteroidea:	
Bathybiaster loripes obesus Sladen	66(1); 89(1).
Leptychaster kerguelenensis kerguelenensis Smith	60(2); 61(1); 84(2); 90(3).
Odontaster meridionalis (Smith)	5(2).
Pteraster affinis lebruni Perrier	5(2).
Porania antarctica antarctica Smith	29(1).
P. antarctica glaber Fisher	5(1); 8(3).
Anasterias perrieri (Smith)	29(1).
Diplasterias meridionalis (Perrier)	8(3); 113(2).
Labidiaster annulatus Sladen	29(1).
Smilasterias scalprifera (Sladen)	5(3).
Holothuroidea:	
Eumolpadia violacea (Studer)	8(4); 10(1); 20(3); 28(2); 42(1); 74(1); 79(3); 81(2); 86(2); 87(3); 89(3).
Pseudocnus laevigatus (Verrill)	5(6); 8(124); 9(1); 10(1); 29(4); 53(141); 55(1).
Staurocucumis liouvillei (Vaney)	5(4); 113(1).
Trachythyone parva (Ludwig)	42(2); 55(1); 74(1); 79(1).
T. denticulata (Ekman)	53(1).
Psolidium incertum (Théel)	5(1).
Heterocucumis georgiana (Lampert)	90(1).
Chiridota sp.	84(1).
Psolus sp.	90(1).
Cucumaria sp.	53(1).
Ophiuroidea:	
Ophiacantha vivipara Ljungman	5(1); 10(1); 53(7).
O. imago Lyman	5(11); 53(22); 90(2); 113(1).
Ophioparva blochi n.g., n.sp.	5(13); 54(4).
Amphiura angularis angularis Lyman	5(1).
A. angularis protecta Hertz	5(4); 8(21); 29(1); 79(1); 89(1); 90(7).
A. antarctica Studer	5(10); 8(157); 9(2); 10(16); 19(1); 60(3); 79(1); 90(12); 113(12).

A. joubini Koehler	55(3); 56(4); 105(3); 107(2).
A. tomentosa Lyman	5(2); 54(3).
Toporkovia antarctica (Lyman)	5(1).
Ophiomisidium speciosum Koehler	5(9); 54(1); 56(2); 66(1); 114(1).
Ophionotus hexactis (Smith)	8(1); 10(3); 19(2); 39(10); 42(6); 60(19).
Ophiogona laevigata Studer	85(5); 107(5).
Ophiurolepis carinata (Studer)	5(3); 90(1).
Ophiura brevispina (Smith)	5(1); 8(41); 9(1); 20(1); 60(1); 79(3); 84(6); 89(10); 90(1).
O. ambigua (Lyman)	5(3); 90(4); 113(1); 114(2).
O. amitina (Lyman)	54(4); 55(1); 85(1); 92(1); 97(5); 115(16).
O. hastata (Lyman)	105(1).

Table 2. Station Co-ordinates and depths

St.No.	Co-ordinates	Depth	St.No.	Co-ordinates	Depth	St.No.	Co-ordinates	Depth
5	49°30.0′S : 70°56.0′E;	147 m	53	48°30.0′S : 68°16.0′E;	155 m	85	49°06.2′S : 70°13.2′E;	50 m
8	49°31.2′S : 69°38.3′E;	22 m	54	48°19.0′S : 67°56.5′E;	192 m	86	49°02.9′S : 69°58.0′E;	95 m
9	49°32.2′S : 69°39.4′E;	111 m	55	48°11.2′S : 67°41.9′E;	275 m	87	48°55.2′S : 70°00.0′E;	106 m
10	49°33.2′S : 69°40.8′E;	58 m	56	48°05.4′S : 67°28.1′E;	39 m	89	48°38.0′S : 70°06.0′E;	105 m
12	49°39.8′S : 69°43.1′E;	36 m	60	48°41.0′S : 69°02.2′E;	17 m	90	48°20.9′S : 70°09.0′E;	128 m
18	49°35.2′S : 69°20.0′E;	18 m	61	48°40.5′S : 69°03.6′E;	50 m	92	47°44.8′S : 70°15.7′E;	167 m
19	49°36.1′S : 69°20.7′E;	70 m	62	48°40.6′S : 69°11.3′E;	61 m	94	47°26.5′S : 70°23.8′E;	170 m
20	49°37.9′S : 69°20.2′E;	117 m	66	47°41.5′S : 69°00.0′E;	202 m	97	46°52.7′S : 70°33.1′E;	920 m
28	49°30.0′S : 69°12.5′E;	89 m	73	49°06.3′S : 69°04.0′E;	30 m	105	48°43.9′S : 71°06.5′E;	843 m
29	49°31.0′S : 69°11.7′E;	23 m	74	49°02.3′S : 69°01.1′E;	31 m	107	48°32.3′S : 71°18.5′E;	1390 m
30	49°27.7′S : 68°50.1′E;	35 m	75	48°58.1′S : 69°08.0′E;	211 m	110	49°10.0′S : 70°34.0′E;	18 m
31	49°27.3′S : 68°46.5′E;	68 m	77	48°51.3′S : 69°10.3′E;	185 m	113	49°51.0′S : 70°19.8′E;	145 m
39	49°08.8′S : 68°54.0′E;	80 m	79	49°04.0′S : 69°21.3′E;	43 m	114	49°54.5′S : 70°24.4′E;	168 m
42	49°09.3′S : 68°46.8′E;	142 m	81	48°57.6′S : 69°28.0′E;	230 m	115	49°59.0′S : 70°29.6′E;	252 m
49	48°48.2′S : 68°50.2′E;	65 m	84	49°08.3′S : 69°56.5′E;	50 m	121	49°41.8′S : 70°08.1′E;	16 m

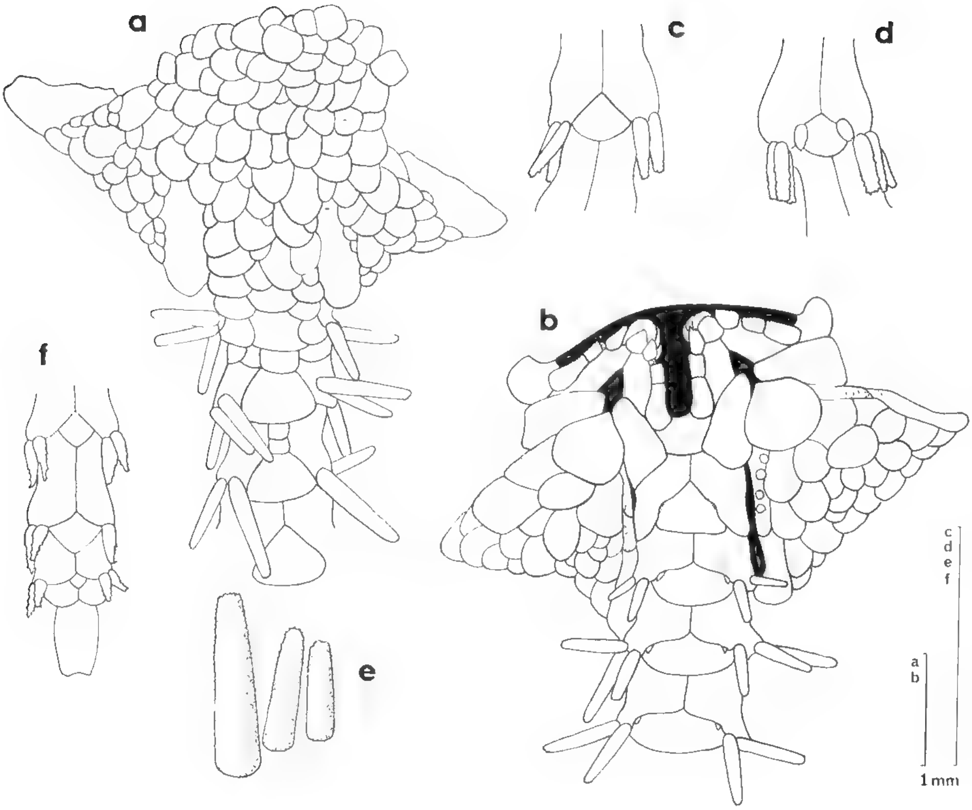

Fig. 2. *Ophioparva blochi* n. gen., n.sp.: **a.** dorsal view; **b.** ventral view; **c.** dorsal view of an arm (13th segment); **d.** ventral view of an arm (13th segment); **e.** arm spines (7th segment); **f.** dorsal view of the end of an arm.

which is broadly contiguous with the first lateral arm plate without arm spines. Proximally the adoral shields and oral plates leave an obvious diastema, the latter only joined in their proximal third. These oral plates are subtriangular, more than twice as long as wide; they bear three lateral oral papillae, the distal papilla the largest rectangular, the middle one also rectangular but shorter, the proximal papilla conical. This proximal papilla is separated from the middle one by a short diastema when the buccal orifice is broadly open in larger sized specimens. There is an unpaired infradental papilla, more developed than the proximal lateral papillae, conical or more or less rounded at the tip; this is immediately beneath a row of 4-5 oval, well-developed dental papillae. The oral and dental papillae are bordered by very fine denticles. The contiguous oral papillae are capable of completely closing the buccal orifice (figs. 2b and 3b).

The first two or three dorsal arm-plates are separated by one or two small rectangular plates, the following dorsal arm plates by lateral plates which become more and more broadly joined on the median line (fig. 2c). The dorsal arm-plates are triangular, the distal edge broadly convex, the proximal angle acute, as wide as long. Towards the distal end of the arm, they become smaller and smaller, although the segments become longer. (fig. 2f). The first ventral arm-plate is pentagonal; the next, larger, is triangular, as wide as long, the distal edge almost straight, the lateral edges convex to the level of the scarcely visible tentacle pore which is without tentacle

scales, the proximal angle sub-acute. The other ventral arm-plates are oval, more than twice as broad as long, the distal edge broadly convex, the proximal edge composed of two sides united by a short acute angle, slightly excavated at the level of the tentacle pore, marked by a tiny pointed tentacle scale (fig. 2d). Towards the end of the arm, the ventral plates become similar in appearance to the dorsal plates, triangular, as long as broad, the distal edge convex, the straight proximal sides joined by a sub-acute angle; the tentacle scale, always single, becomes comparatively more developed, lanceolate and finely denticulate at its extremity. At the end of the arm (fig. 2f) the last two segments become abruptly shorter; the penultimate dorsal and ventral arm-plates become broader while the last ones are much reduced. A long cylindrical, non-segmented section ends the arm.

The arm-spines are raised, 3 in number, cylindrical, slightly narrower and finely denticulate at their extremity. In the proximal part of the arm the dorsal spine is twice as long as the ventral one, which is slightly shorter than the length of the segment. Towards the distal end of the arm the spines become sub-equal, more pointed and more denticulate (fig. 2e).

REMARKS: Specimens of this species were found only in grab samples of two stations and not in the dredge and trawl samples from the same stations or any other stations of the MD04/Benthos cruise.

Although the external skeletal plates are well calcified, their fine granules suggest that the 17 specimens collected were juvenile. But those, whose maximum disc diameter is only 5.5 mm, do not appear to correspond with any species from the sub-antarctic region, or even from the antarctic or Indian Ocean areas. These specimens have not been identified with any known genus, so it is with much hesitation that I place them in a specific family. The characters of *Ophioparva blochi* suggest affinities with several families: the genus *Ophiochytra* of the Amphilepidae by the buccal structure and several other characters, the juvenile Ophiocomidae (for example *Ophiocoma erinaceus)* by the dorsal side of the disc, the Ophiolepidinae by the ventral side of the disc. The link with the Ophiacanthidae is however, most suggested by the arm and buccal structures; sub-rectangular oral papillae occur in certain species of this family.

Family OPHIURIDAE

Ophiomisidium speciosum Koehler

Figs. 3c, d and 4

Ophiomisidium speciosum Koehler, 1914: 34-36, pl. 3, figs 3-4. — Schoener, 1969: 131-133, figs 3-4.

MATERIAL EXAMINED: 9 specimens, st. 5, February 22nd, 1975, 49°30.0'S-70°56.0'E, 147 m, basalt pebbles and shelly sand; 1 specimen, st. 54, March 3rd, 1975, 48°19.0'S-67°56.5'E, 192 m basalt gravel and muddy sand; 2 specimens, st. 56, March 3rd, 1975, 48°05.4'S-67°28.1'E, 390 m, gravel and organic mud; 1 specimen, st. 66, March 12th, 1975, 47°41.5'S-69°00.0'E, 202 m; 1 specimen st. 114, March 15th, 1975, 49°54.5'S-70°24.4'E, 168 m basalt pebbles and sand with bryozoans.

DESCRIPTION: The disc diameters of the 14 specimens measure from 1.5 to 4 mm; the arms, mostly broken, are 5 mm on the largest specimen (incomplete) which is described here.

In dorsal view, the disc appears circular, covered by a small number of large, regular, symmetrical plates (figs. 3c and 4a). The centrodorsal is pentagonal, surrounded by 5 primary plates, much wider than long, trapezoidal, the proximal and distal edges semi-circular. The radial shields are longer than wide, joined proximally, diverging and rounded distally, separated by two small plates: the first of which is triangular, the second semi-circular. A single row of two

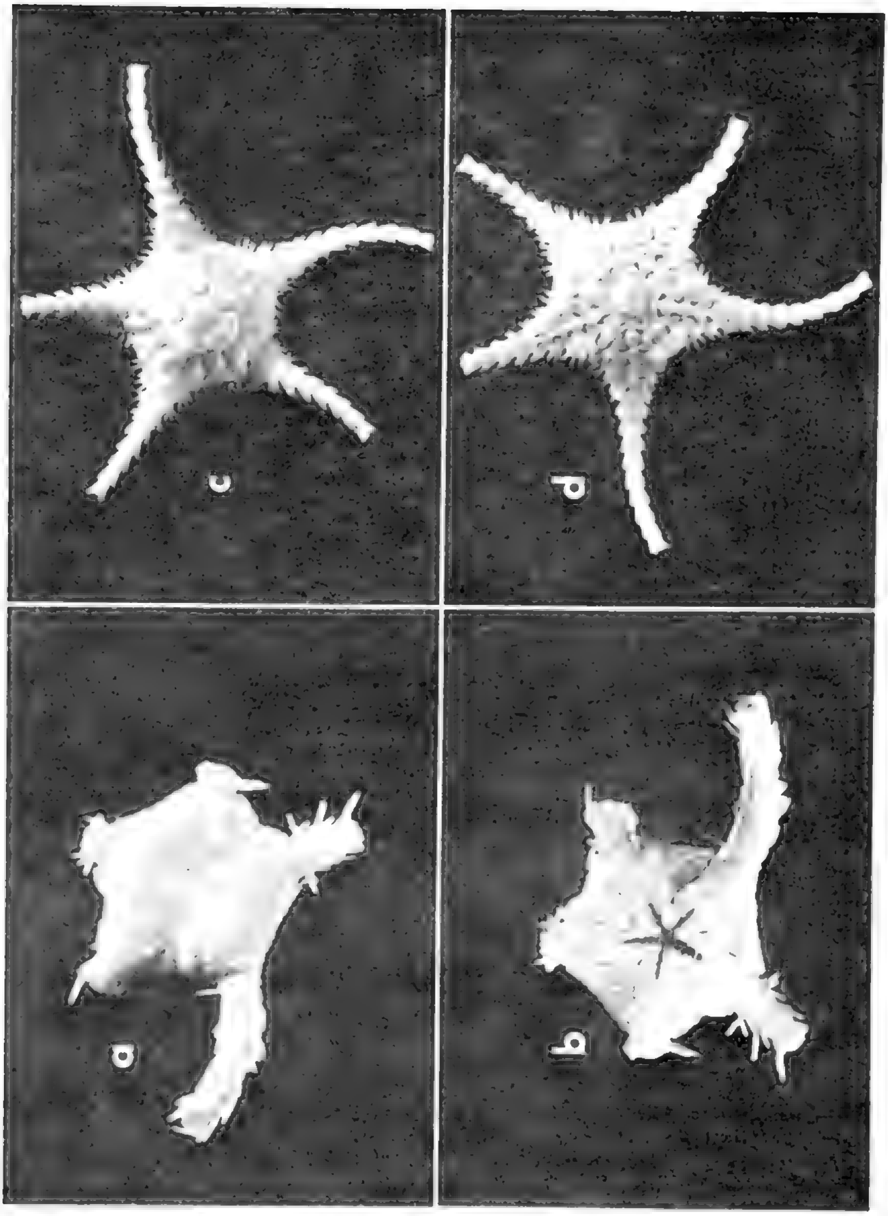

Fig. 3. *Ophioparva blochi* n. gen., n.sp. : **a.** dorsal view; **b.** ventral view. *Ophiomisidium speciosum* Koehler: **c.** dorsal view; **d.** ventral view.

plates covers the interradial spaces, the first rectangular, much longer than wide, the second trapezoidal and enlarged.

In ventral view, the disc appears pentagonal due to the great development of the first three lateral arm-plates. The interradial spaces are much reduced, covered by a large elongated, fan-shaped, plate, the convex distal edge revealing, subjacent, the edge of the marginal dorsal interradial plate; the ventral interradial plate is bordered by two very narrow plates, sometimes almost entirely hidden by the first lateral arm-plates. The oral shields are small, pentagonal, with an acute proximal angle, the subequal sides joined by an obtuse angle, the distal edge straight. Their sides are distally bordered by an elongated genital plate marking a very narrow genital slit. The adoral shields and oral plates are well-developed: the former are trapezoidal, contiguous, the lateral sides slightly indented by the first arm tentacle pore: the latter sub-triangular, bordered by a very long and narrow distal oral papilla, rectangular, preceded by a much shorter proximal papilla, usually small and difficult to see. The pointed single terminal papilla is likewise small (figs. 3d and 4b).

The first dorsal arm-plate is larger than the following ones, rectangular, sometimes pentagonal, wider than long. The following plates are triangular, with an acute proximal angle, the distal edge slightly convex: further along the arm they become smaller and smaller and have almost disappeared after the 10th segment.

The first five ventral arm-plates are large, becoming smaller towards the distal end of the arm, hour-glass shaped, hexagonal with an obtuse proximal angle, the distal edge broadly convex, the sides excavated at the level of the tentacle pores. The tentacle pores are wide, circular, bordered by a large, sometimes double, oval tentacle scale. Beyond the fifth segment the tentacle pores disappear and the ventral arm-plates become abruptly triangular, of a similar shape to the dorsal arm-plates. They become smaller along the arm, and disappear beyond the 10th segment.

In ventral view, the first four lateral arm-plates are much larger than the rest, of decreasing size, trapezoidal. The distal end of the second pair, sometimes the spines of the first, are visible in dorsal view, beyond the edge of the disc. These first four pairs of lateral arm-plates are barely joined ventrally; dorsally only the fourth pair is much in contact, like the following plates which become much narrower and longer, giving the arm a fusiform appearance. After the fifth segment, like the dorsal and ventral arm-plates, the appearance of the lateral arm-plates is similar on both dorsal and ventral surfaces.

There are two spines on the first arm-segment, then three on all others. These spines are subcylindrical, squat, and are armed with spinelets distally (fig. 4c). They become shorter and shorter along the arm.

Seen under a binocular microscope, the disc and arm-plates appear granular.

REMARKS: Six species of the genus *Ophiomisidium* are presently known, but none has been commonly collected. The species appear to have restricted distributions (fig. 5): *O. pulchellum* (W. Thomson) from the south Atlantic, close to the South Africa coast (275 to more than 3000 m), *O. flabellum* (Lyman) from the Sydney coastal region (60 m), *O. leurum* Ziesenhenne from similar coastal regions of the Galapagos Islands and Chacahua Bay (Mexico) (80-140 m), *O. irene* Fell from the Chatham Islands and Pegasus canyon (New Zealand) (230-1006 m), *O. speciosum* Koehler from the tropical Atlantic (587-1562 m) and *O. mirabile* Smirnov from the Ob Bank (Antarctic part of the Indian Ocean) (240 m).

Three of these species, *O. flabellum*, *O. irene*, and *O. mirabile* are characterised by a great development of the first pair of lateral arm-plates which, ventrally, are joined at the back of the

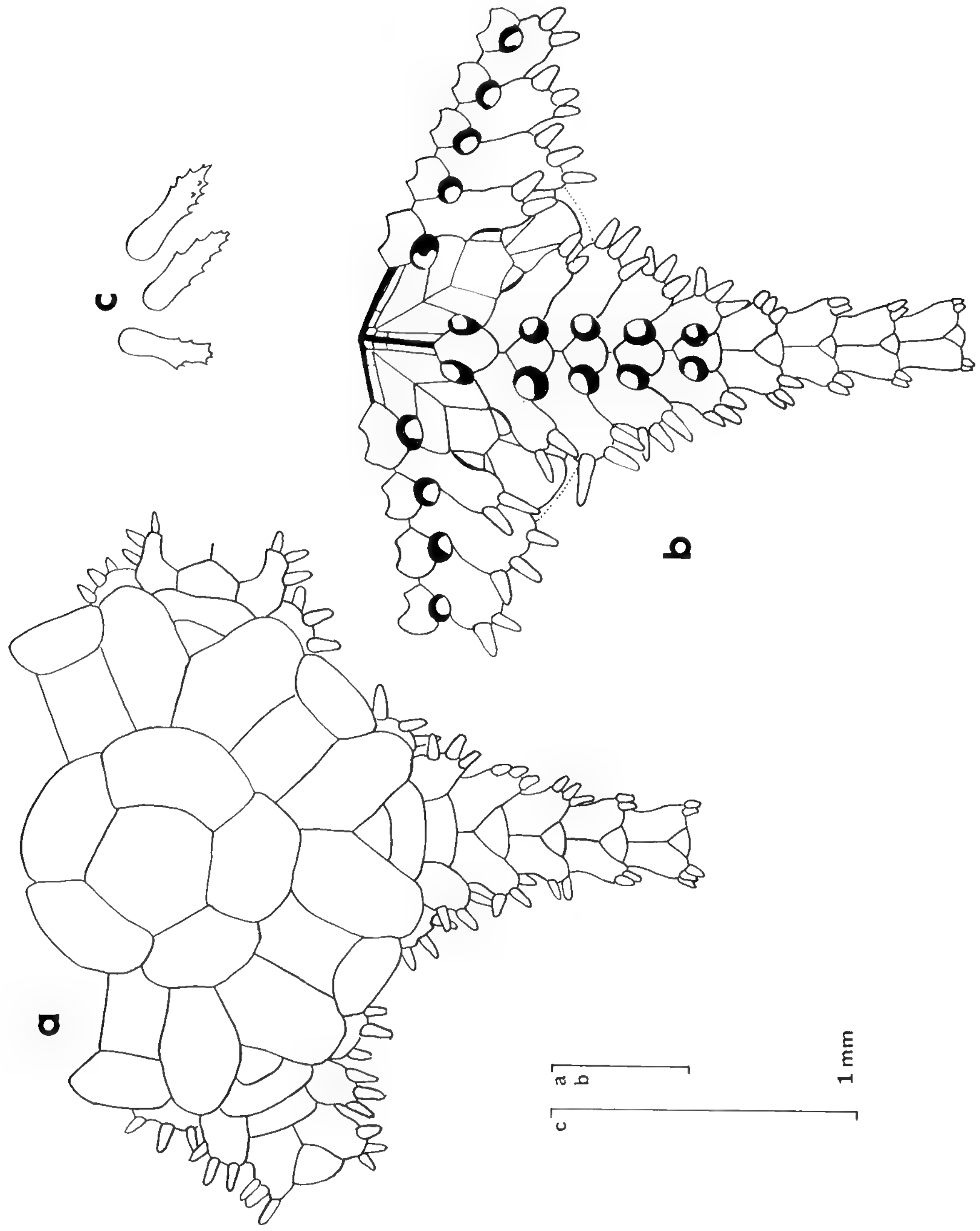

Fig. 4. *Ophiomisidium speciosum* Koehler: **a.** dorsal view; **b.** ventral view; **c.** arm spines (2nd segment).

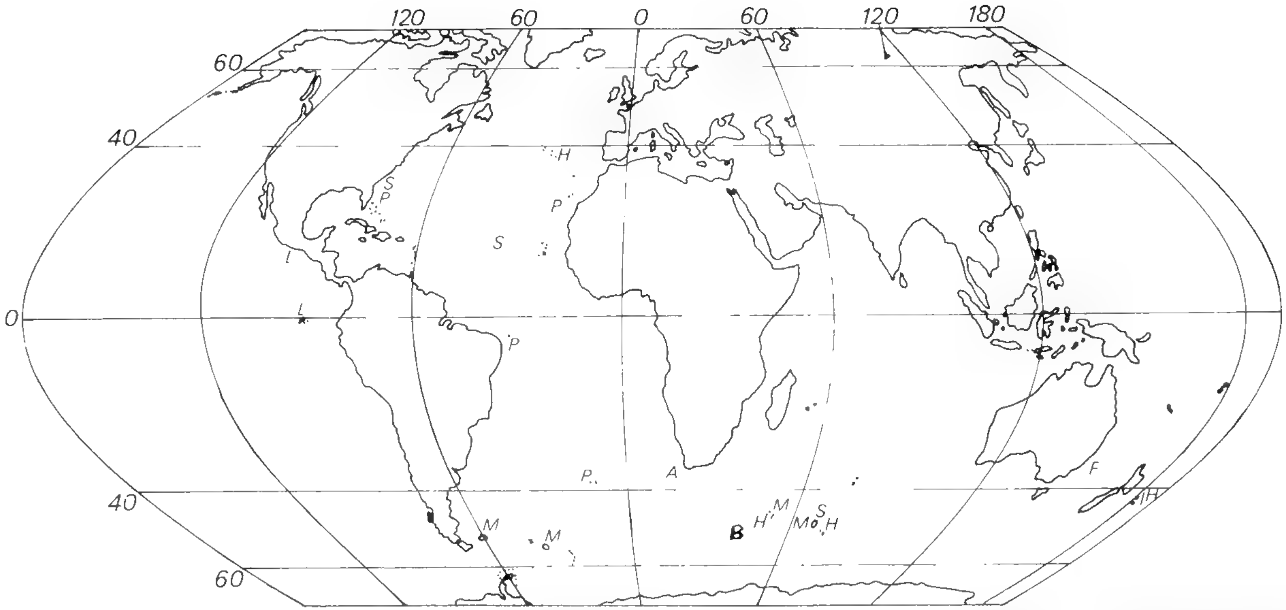

Fig. 5. Geographic distribution of species of genus *Ophiomisidium* and of three species of genus *Ophiura:* **a.** *Ophiura affinis simulans* (Mortensen); **b.** *Ophiomisidium mirabile* Smirnov; **f.** *Ophiomisidium flabellum* (Lyman); **h.** *Ophiura hastata* (Lyman); **i.** *Ophiomisidium irene* Fell; **l.** *Ophiomisidium leurum* Ziesenhenne; **m.** *Ophiura amitina* (Lyman); **p.** *Ophiomisidium pulchellum* (W. Thomson); **s.** *Ophiomisidium speciosum* Koehler.

much reduced oral shield. The three other species, as is characteristic of the genus *Ophiomisidium*, also have the first lateral arm-plates well-developed, but these are no longer joined and reveal, distal to the oral shield, one to three interradial plates. The genital slits are present only in *O. pulchellum* and *O. speciosum* but Fell (1960) and Baker (1977) record, in new material of *O. irene*, the appearance of tiny genital slits on the largest specimen.

The specimens examined here, agree closely with the original diagnosis of *O. speciosum*. However, Koehler's holotype and five paratypes, housed at the USNM and kindly lent to me by Maureen Downey for examination, are missing a well-developed and rectangular first dorsal arm-plate; this is also missing from my larger specimens. Also, the surface of the disc plates, like the arms of the types, are much more granular than those of the Kerguelen specimens. These two differences however, seem merely to represent intraspecific variation. The evolution of the skeleton structure of *O. speciosum* as a function of size as shown by Schoener (1969), and the appearance of genital slits in the larger specimens of *O. irene* suggests that the criteria used to distinguish the species of the genus *Ophiomisidium* may need reconsidering. The discovery of *O. speciosum* on the continental shelf of the Kerguelen islands and the variability described above, suggests that some of the other "species" of *Ophiomisidium* may not, in fact, be separable from one another. Thus, the only other antarctic species of the genus, *O. mirabile* Smirnov (1977), is very close to *O. irene*, and according to Baker (1977) *O. flabellum* and *O. irene* can be distinguished only by the number and the size of the upper disc-plates and in the shape and relief of the plates on the underside.

The other two genera at present placed in the family Ophiuridae (Ophiurinae), *Astrophiura* Sladen and *Ophiophycis* Koehler are also characterised by the large first lateral arm-plates. With the genus *Ophiomisidium* they could be considered to form a distinct family, the Astrophiuridae Sladen (Cherbonnier and Guille, 1976).

Ophiura amitina (Lyman)

Figs 6a-c and 7c, d

Ophiocten amitinum Lyman, 1878: 100, pl. 5, figs 129-130; 1882, 79, pl. 9, figs 7-9. — Studer, 1885: 16, pl. 2, figs 8a-f. — Koehler, 1907: 288; 1923: 122. — H. L. Clark, 1915; 328. — Mortensen, 1936: 335, fig. 48a. — Madsen, 1967: 138. — Fell, Holtzinger and Sherraden, 1969: pl. 26, map 2. — A. M. Clark and Courtman-Stock, 1976: 192.

MATERIAL EXAMINED: 1 specimen, st. 85, March 9th, 1975, 49°06.2'S-70°13.2'E, 50 m, basalt gravel and pebbles, organic muddy sand; 1 specimen, st. 92, March 10th, 1975, 47°44.8'S-70°15.7'E, 164 m, basalt gravel and pebbles, green muddy sand; 4 specimens, st. 54, March 3rd, 1975, 48°19.0'S-67°56.5'E, 92 m, basalt gravel and muddy sand; 16 specimens, st. 115, March 15th, 1975, 49°59.0'S-70°29.6'E, 252 m, fine sand with bryozoans; 1 specimen, st. March 3rd, 1975, 48°11.2'S-67°41.9'E, 275 m, fine sand, 5 specimens, st. 97, March 11th, 1975, 46°52.7'S-70°33.1'E, 920 m, mud. (d.d. range 3-7 mm).

REMARKS: Two species of the genus *Ophiocten* are known from the southern part of the Indian Ocean: *O. amitinum* Lyman from the Kerguelen islands and *O. hastatum* Lyman. Examination of the "Challenger" types, deposited in the British Museum and loaned to me by A. M. Clark, reveal several errors in Lyman's diagnoses and figures, which have doubtless led to confusion of the species.

Lyman, in effect, distinguishes the two species mainly by the presence of sub-equal arm-spines, a smaller, more triangular first ventral arm-plate in *O. amitinum*, and oral papillae of different shapes. In fact, in all the specimens of *O. amitinum* from the "Challenger", the first arm-segments bear an upper spine thicker and twice as long as the next two; the oral papillae and

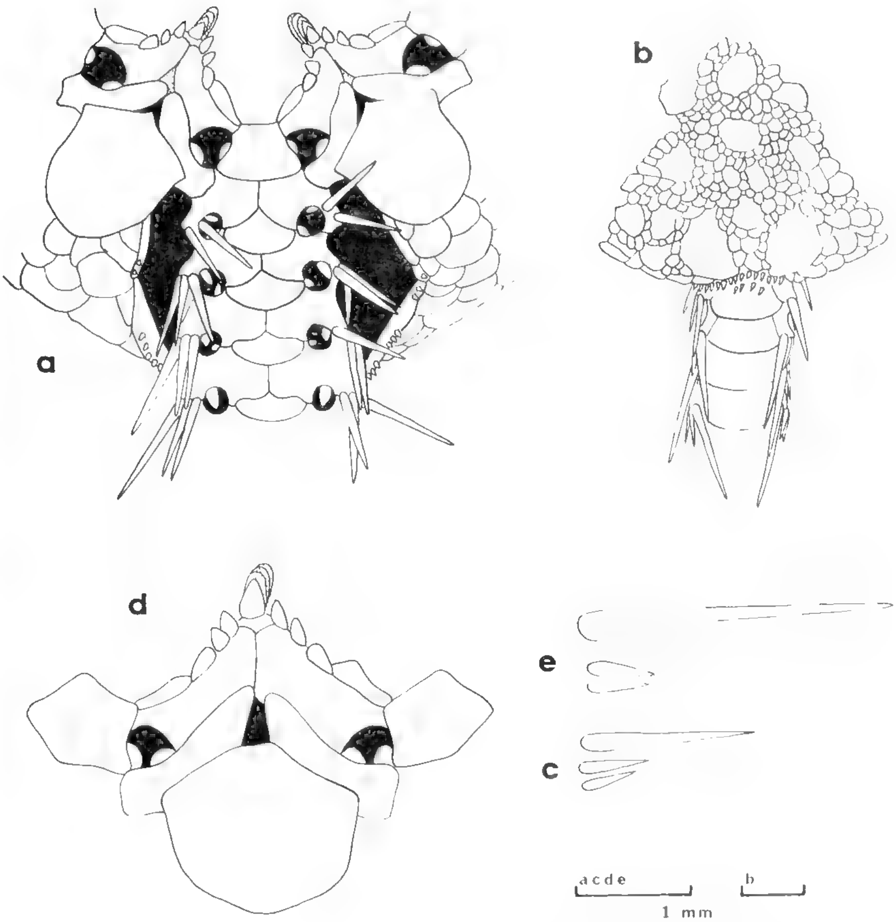

Fig. 6. *Ophiura amitina* (Lyman): **a.** ventral view; **b.** dorsal view; **c.** arm spines (5th segment). *Ophiura hastata* (Lyman): **d.** one jaw; **e.** arm spines (5th segment).

the first ventral arm-plate are similar to those of *O. hastatum*.

As a further point of confusion, two sub-species of *O. amitinum*, *O. amitinum microplax* and *O. amitinum simulans* were distinguished by Mortensen (1933, 1936) and their distribution seems limited to South Africa. However, A. M. Clark and J. Courtman-Stock (1976) showed that these two sub-species should really be reunited and linked with the north Atlantic *Ophiura affinis*. These two authors stress that the distinction between the genera *Ophiura* and *Ophiocten* is "clearly very slight with *Ophiura affinis* bridging the gap between them".

While the forms *hastatum*, *amitinum* and *affinis simulans* are very distinct (Table 3), they appear too close to be generically separated. Until there has been a worldwide revision of the generic limits of the family Ophiuridae, these three forms must be placed in the same genus *Ophiura*, as A. M. Clark and J. Courtman-Stock have already concluded for one of them.

Ophiura amitina is considered by Madsen (1967) as a common circumpolar species, principally sub-antarctic, but in the South African region it is replaced by *O. affinis simulans* (Fig. 5) which is very abundant in some biotopes (Day, Field and Penrith, 1970).

Ophiura hastata (Lyman)

Figs 6d, e and 7a, b

Ophiocten hastatum Lyman, 1878: 103, pl. 5, figs 133-134; 1882: 82, pl.9, figs 10-11. — Koehler, 1898: 42, pl.7, figs 32-33. — Fell, 1958: 29.

Ophiocten longispinum Koehler, 1896a: 204; 1896b: 243.

MATERIAL EXAMINED: 1 specimen, st. 105, March 13th, 1975, 48°43.0′S-71°06.5′E, 843 m, mud (d.d. = 13 mm).

REMARKS: *Ophiura hastata* does not appear to have been found since the expeditions of the "Challenger" and "Hirondelle", and is known from widely separated localities, and from only a few specimens: the central Atlantic (Azores), the southern Indian Ocean and New Zealand, always at depths of more than 1800 m. The discovery of *O. hastata* at only 843 m is an important extension of bathymetric range.

As I have indicated in the discussion about the taxonomic problems relating to *O. amitina*, the similar characteristics of these two species and the errors in Lyman's descriptions have caused confusion between them, and this explains to some extent the absence of data on *O. hastata*. In presently available collections *O. hastata* can be easily distinguished from *O. amitina* by the ornamentation of the dorsal face of the disc, the wider than long oral shields, and the very long upper arm-spine. But one must also note that all the known specimens of *O. hastata* are of a larger size than those of *O. amitina*.

BIOGEOGRAPHY OF SPECIES COLLECTED

Except for the discovery of *Ophioparva blochi* and *Ophiomisidium speciosum*, the species collected have a wide antarctic and sub-antarctic distribution, or are endemic to the Kerguelen islands or the Kerguelen province, as defined by Koehler (1912), which includes Heard, Crozet, Marion and Prince Edward Islands. However these endemic species are very closely related to circum-antarctic species.

Thus, the single species of crinoid collected, *Promachochrinus kerguelensis*, is the most widespread and abundant crinoid in the antarctic and sub-antarctic region between 10 and 1080 metres deep. Three of the four echinoids are endemic to the Kerguelen islands; one, *Ctenocidaris nutrix*, has also been found around the Crozet islands. The number of asteroid species is low compared with previous studies, probably due to the sampling method used. Their collection was in fact, almost limited to two stations: one at the south-east of the archipelago, at the base of the fjord of Table Bay (st. 29, 23 m), the other at the entrance of Royal Pass leading to the Morbihan Gulf (st. 5, 147 m). Of the asteroids, only *Anasterias perrieri* is endemic. Two of the ophiuroids are similarly endemic, and are also the most common and most abundant ophiuroids in the littoral sedimentary substrates: *Amphiura antarctica* (synonymous with *A. eugeniae* Koehler 1917) and *Ophiura brevispina*. *Amphiura joubini* is only found at Kerguelen at depths of more than 275 metres, although this species, littoral in the Antarctic, is considered by Fell et al. (1969) as the only eurythermal form of a stenothermal genus (*Hemilepis*). Of the holothurians identified, only *Eumolpadia violacea* is endemic and similarly very common in the muddy substrates to a depth of 250 metres.

ASSESSMENT OF QUANTITATIVE DATA OF SPECIES COLLECTED

Thirty-four of the forty-two species collected were only present at one to five of the sixty-three stations sampled, and their densities were always low; eight other species were more

Table 3. Relationships between *Ophiura hastata*, *O. amitina* and *O. affinis simulans*

Ophiura hastata (figs. 6d-e; 7a-b)	*Ophiura amitina* (figs. 6a-e; 7c-d)	*Ophiura affinis simulans* (fig. 7e-f)
Radial shield separated slightly divergent; l/w = 3/1; l = +1/3r	Radial shields small, separated, proximally divergent; l/w = 5/3; l = −1/3r	Radial shields separated, slightly divergent; l/w = 2/1; l = +1/3r
Centrodorsal and primary plates little-developed, and barely visible	Centrodorsal and primary plates well-developed, obvious	Centrodorsal and primary plates well-developed, obvious
Spines of arm-combs not more than twice as long as wide	Spines of arm-combs not more than twice as long as wide	Spines of arm-combs spiniform more than three times as long as wide
Oral shields more wide than long or as long as wide	Oral shields longer than wide	Oral shields longer than wide
Upper arm-spine of first proximal segments thickened more than 4 times longer than the next two	Upper arm-spine of first proximal segments thickened more than twice as long as the next two	Arm-spines sub-equal
Upper surface of arm convex	Upper surface of arm convex	Upper surface of arm carinate
d.d. 8 to 14 mm	d.d. 3 to 8 mm	d.d. to 7.5 mm

(l and w = length and width of radial shields; r = ray of disc; d.d. = diameter of disc).

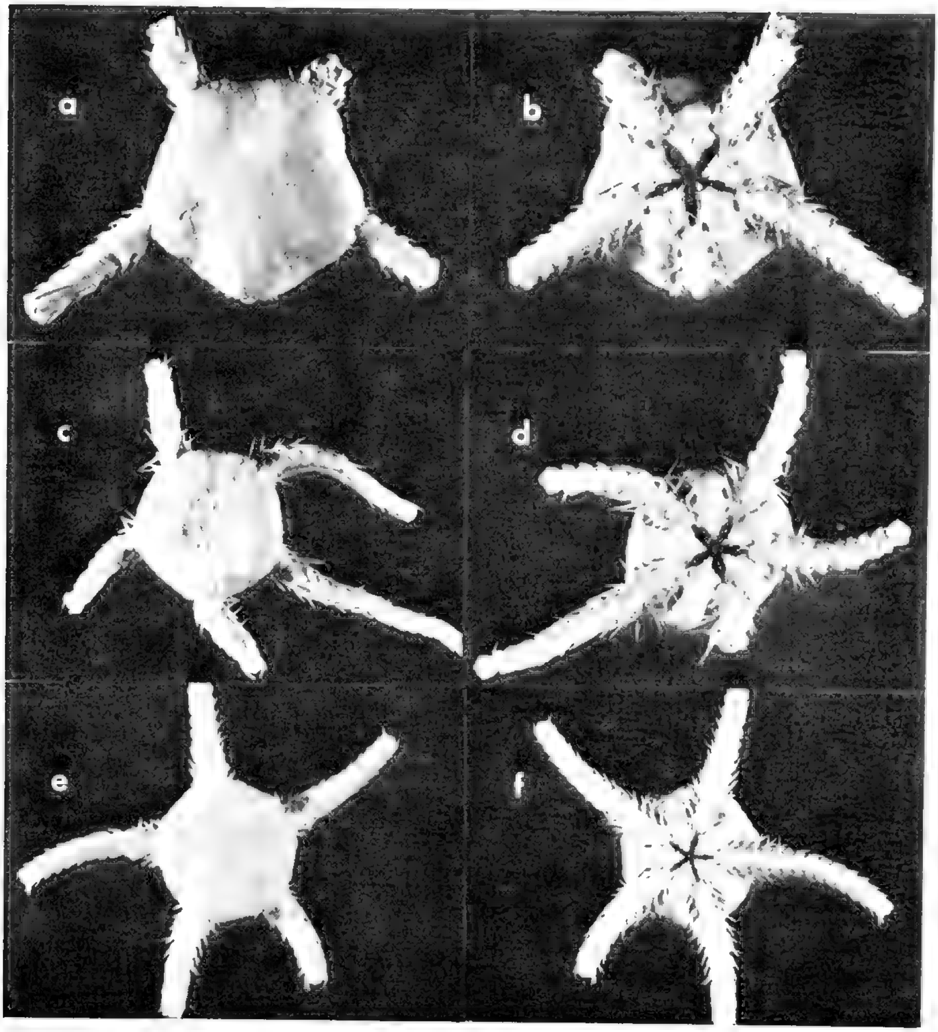

Fig. 7. *Ophiura hastata* (Lyman) (type Challenger 82, 12, 23, 352, British Museum): **a.** dorsal view; **b.** ventral view. *Ophiura amitina* (Lyman) (type Challenger Kerguelen 82, 12, 23, 346, British Museum): **c.** dorsal view; **d.** ventral view. *Ophiura affinis simulans* (Mortensen) (type Discovery South Africa 1936, 12, 30 144, British Museum): **e.** dorsal view; **f.** ventral view.

common.

The crinoid *Promachochrinus kerguelensis*, present at eight stations between 18 and 200 metres depth, had a maximum density of 8 specimens/m^2 (st. 5, 147 m). *Abatus cordatus* is the most common echinoderm at Kerguelen, present at 17 stations, at 8-147 metres depth and reaching a density of 32 specimens/m^2 at the mouth of Lac Marville, at the east of the archipelago, at 18 metres depth. The density of this euryhaline urchin is also relatively high in the sands of the lower intertidal zone where many juveniles occur (Guille and Lasserre, 1979). The ophiuroid *Ophionotus hexactis*, common throughout the antarctic and sub-antarctic, was present in only six stations.

It had a maximum density of 38 specimens/m^2 in mud, at 18 metres depth, in the small bay

of Port Christmas at the far north of Kerguelen (st. 60).

One station (st. 8) in the south of Kerguelen at the base of the fjord of Swains Bay, at a depth of 22 metres and in mud, yielded the highest densities of the five other most common species: *Sterechinus diadema* (6 specimens/m², present at 8 other stations), *Amphiura antarctica* (314 specimens/m², present at 8 other stations), *Ophiura brevispina* (82 specimens/m², present at 7 other stations), *Eumolpadia violacea* (8 specimens/m², present at 10 other stations) and *Pseudocnus laevigatus* (248 specimens/m²). This last holothurian, present at 6 other stations, was more abundant at one of these others (st. 53), situated at the north west of Kerguelen, 162 metres depth, in pebbles and basalt blocks (282 specimens/m²).

Station 8 also had the highest total density of echinoderms with 958 specimens/m² for 14 species present. The station yielding the highest number of species, with 25 species/0.5 m² for 218 specimens/m², was in the open sea, to the east of the archipelago, opposite the entrance of Royal Pass which gives access to Morbihan Gulf, a pass usually swept by strong oceanic currents (st. 5, 147 m). Because of the sudden shoaling here, upwellings are frequently produced.

The average densities of species and specimens for all the 49 stations where echinoderms were present, are respectively 3.7 species/0.5 m² and 52.8 specimens/m². These results, or more precisely those limited to the same bathymetrical range as the data obtained in Morbihan Gulf, indicate, by comparison with the latter (Table 4), a greater density of species and a lower numerical density in the stations outside the gulf, really a separate sea, with a surface of 700 km². The significance of these differences is even more evident if the data obtained in the MD04/Benthos stations situated in fjords is separated from those from stations on the continental shelf (Table 4; fig. 8).

The diversity of the echinoderms is thus greater, and their numerical density lower on the exterior continental shelf than in the protected fjords and bays. This qualitative and quantitative distribution is related to the topography and its effect on hydrological circulation. In fact, the fauna of fjords and interior gulfs is relatively isolated from the strong oceanic currents where as the exterior continental shelf benefits from the supply of nutritive salts and planktonic larvae from the oceanic environment. The south coast of Kerguelen, comprised partly of fjords (e.g. the very rich station 8) is enriched by the general south-west to north-east direction of hydrological circulation (Murail et al., 1977; fig. 8).

The kind of distribution shown by the echinoderms at Kerguelen has been noted for other groups of benthic invertebrates, for example the ascidians (Monniot, 1979). However, it is still only a preliminary observation, obtained from few samples. Some stations, moreover, are exceptions such as station 53 (162 m) at the north east of Kerguelen where the numerical density is markedly raised due to the abundance only of the holothurian *Pseudocnus laevigatus*, whose mode of reproduction produces a patchy distribution.

Thus, the collection from the MD04/Benthos cruise confirms again the qualitative and quantitative richness of the echinoderm fauna of the Kerguelen islands (Guille, 1977a).

ACKNOWLEDGEMENTS

The programme of investigation of the benthos of the continental shelf of the Kerguelen islands is made possible under the scientific Director, Jean-Paul Bloch, of the administration of "Terres Australes et Antarctiques Francaises". I thank G. Cherbonnier for identification of holothurids species, Miss A. M. Clark (British Museum) and Miss Maureen Downey (Smithsonian Institution) for loans of type species and advice, Miss Janet Marshall (Australian Museum) and Professor Lowell Thomas (University of Miami) for the translation of my French paper.

Table 4. Summary of species and specimen densities from Guille (1977a) and this work

	Bathymetric range	Number of samples	Number of species	Average density of species	Average density of individuals
Morbihan Gulf (Kerguelen I.) Smith McIntyre grab 0.1m^2 (Guille, 1977a)	5-180 m	130	36	2.9 sp/0.1 m^2	137.7 ind./m^2
Kerguelen I.	10-1390 m	49	42	3.7 sp 0.5m^2	52.8 ind. m^2
Okean grab, 0.5 m^2 (this work)					
Stations at depths comparable to Morbihan Gulf stations	10-180 m	38	40	4.3 sp/0.5m^2	62 ind./m^2
Stations in fjords	10-230 m	17	18	3.6 sp/0.5 m^2	75.5 ind./m^2
Stations in open sea	18-1390 m	32	33	4.2 sp/0.5 m^2	36.7 ind./m^2

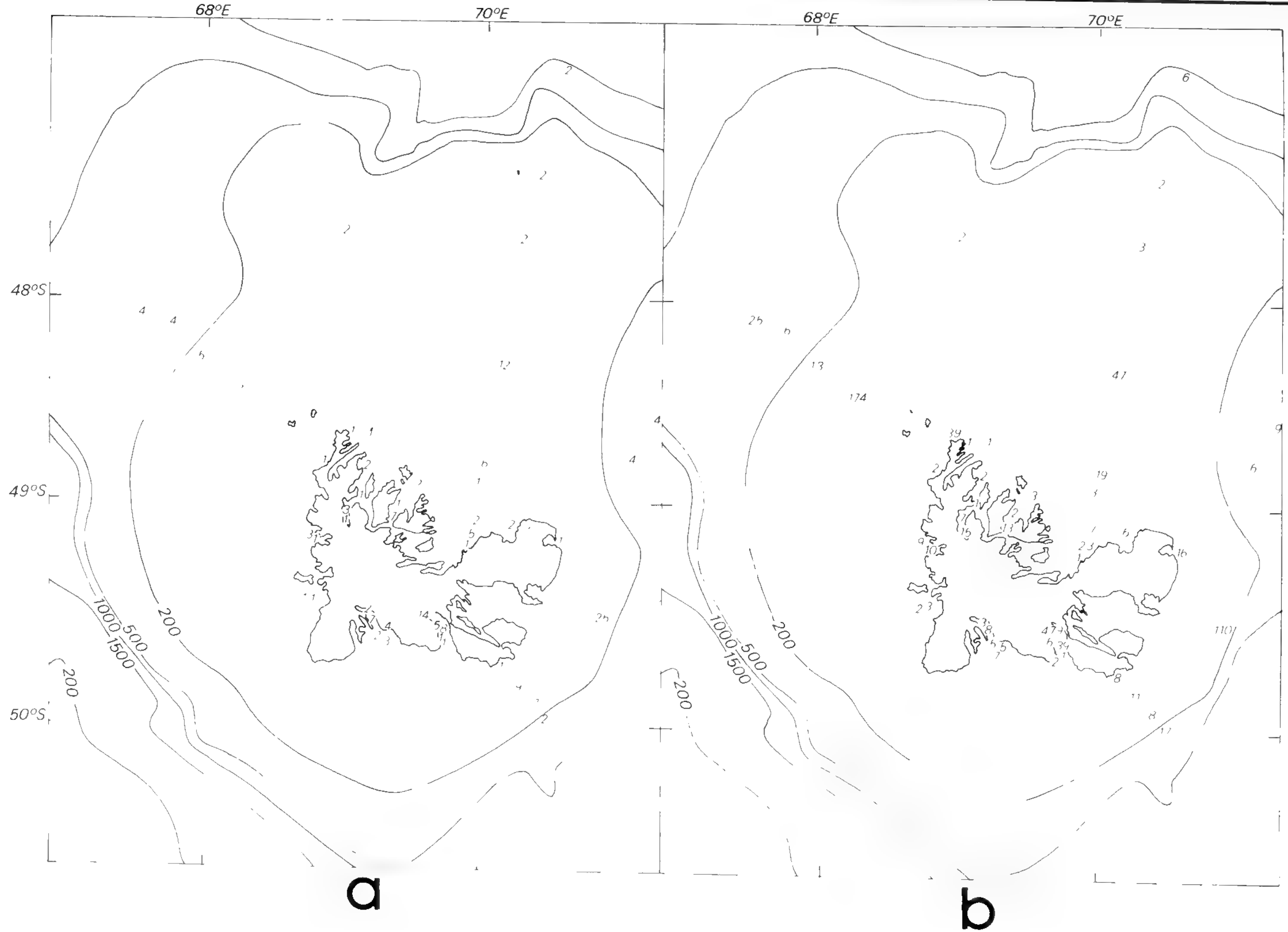

Fig. 8. Maps of grab samples of MD04/Benthos cruise: **a.** number of echinoderm species in each station for 0.5 m²; **b.** number of Echinoderm individuals in each station for 0.5 m².

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6. A REVISION OF THE ASTERINID GENUS *NEPANTHIA* GRAY, 1840 (ECHINODERMATA: ASTEROIDEA), WITH THE DESCRIPTION OF THREE NEW SPECIES

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SUMMARY

The genus *Nepanthia* Gray, 1840 is revised and eight species recognised, including three new species, one from New South Wales, one from north of Sabah, Borneo and one form the Sulu Sea, Philippines. Fisher's opinion that *Parasterina crassa* should be referred to *Nepanthia* is supported and the species is here included. Variation in the species *N. belcheri* (Perrier) is discussed and the species *N. brevis* (Perrier), *N. suffarcinata* Sladen, *N. joubini* Koehler, *N. variabilis* H. L. Clark and *N. magnispina* H. L. Clark are considered conspecific with it. A key is given for the eight species recognised.

INTRODUCTION

Gray (1840; 1866), described the genus *Nepanthia*, in the family Pentacerotidae, for two species *N. tessellata* (from an unknown locality) and *N. maculata* (From Migupou, Philippine Islands).

Müller and Troschel (1842) referred these species to *Chaetaster* which they described a few months prior to Gray's *Nepanthia* in 1840, considering Gray's species to be congeneric with *C. subulata* (Lamarck) (type-species of *Chaetaster* by monotopy).

Perrier (1875), placed *Chaetaster* in the family Astropectinidae, synonymising *Nepanthia tessellata* with *C. longipes* (Retzius). He considered *Nepanthia* to be a subgenus of *Asterina* (family Asterinidae; in which family it has since remained) recognising the validity of *A. (N.) maculata*, the type-specimen of which he examined. He described two new species *A. (N.) belcheri* and *A. (N.) brevis*. This action leaves *N. maculata* as type species of *Nepanthia*, failing Gray's nomination of a type-species from either of the two he included in his genus.

Viguier (1878), placed *Chaetaster* in the family Linkiadae of his subclass of asteroids (Stellérides) "Astéries adambulacraires" (characterised by the predominence of the adambulacral plates in the mouth ring), listing *Nepanthia* as a synonym of *Chaetaster*. He did not discuss the genus or its species.

Perrier (1884), in his remarkable classification of asteroids, based on the form of the pedicellariae, without comment listed *Nepanthia* in the family Asterinidae, Order "Stelleridae Spinulosae" (p. 164, referred to as Echinulatae in subsequent pages).

Sladen (1889), considered the skeletal features of the species of *Nepanthia* to be sufficiently distinctive to "warrant the retention of *Nepanthia* as an independent genus", in the family Asterinidae (subfamily Asterininae) of the new order Phanerozonia.

Gray, 1847 described *Patiria? crassa* from Western Australia in a third group of species (*P. ocellifera*, *P. obtusa* and *P. ? crassa*) of his genus *Patiria*. These were characterised by having 5

TABLE 1. Status of Species referred to *Nepanthia* Gray

Species Type Locality	History to Present	Present Status in *Nepanthia*
Nepanthia tessellata Gray, 1840 unknown	Referred to *Chaetaster*, Müller & Troschel, 1842; a synonym of *C. longipes* acc. Perrier 1875	—
Nepanthia maculata Gray, 1840 Migupou, Philippines	Referred to *Chaetaster*, Müller & Troschel, 1842; to *Asterina (Nephanthia)*, Perrier, 1875; to *Nepanthia*, Sladen, 1889	Valid species of *Nepanthia* after Gray, 1840
Patiria ? crassa Gray, 1847 Western Australia	Referred to *Asterina (Nepanthia)*, Perrier, 1875; to *Parasterina*, Fisher, 1908; to *Nepanthia*, Fisher, 1941; to *Parasterina*, H. L. Clark, 1946	Referred herein to *Nepanthia*, after Fisher, 1941
Asterina (Nepanthia) belcheri Perrier, 1875 unknown	Referred to *Nepanthia*, Sladen, 1889	Valid species of *Nepanthia*, after Sladen, 1889
Asterina (Nepanthia) brevis Perrier, 1875/Prince of Wales Strait, Torres Strait, N. Queensland, Australia	Referred to *Nepanthia*, Sladen, 1889	A synonym of *N. belcheri*, herein
Nepanthia suffarcinata Sladen, 1889 Mergui Archipelago, Burma	—	A synonym of *N. belcheri*, herein
Patiria briareus Bell, 1894 Macclesfield Bank, South China Sea	Referred to *Nepanthia*, A. M. Clark 1956	Valid species of *Nepanthia*, after A. M. Clark, 1956
Nepanthia joubini Koehler, 1908/ Cap St. Jacques, Cochin China (Vietnam)	—	A synonym of *N. belcheri*, herein
Henricia heteractis H. L. Clark, 1909/ Lord Howe Island, Tasman Sea	A synonym of *N. belcheri*, H. L. Clark, 1938	As H. L. Clark, 1938
Nepanthia brachiata Koehler, 1910a Andaman Islands, Indian Ocean	Referred to *Paranepanthia*, Fisher, 1919	As Fisher, 1919
Nepanthia polyplax Döderlein, 1926 Rockhampton, Queensland, Australia	A synonym of *N. belcheri*, H. L. Clark, 1938	As H. L. Clark, 1938

Parasterina troughtoni Livingstone, 1934/Albany, Western Australia	Referred to *Nepanthia,* A. M. Clark, 1966	As A. M. Clark, 1966
Nepanthia magnispina H. L. Clark, 1938/ Augustus (or Champagny) Island, N.W. Australia	—	A synonym of *N. belcheri*, herein
Nepanthia variabilis H. L. Clark, 1938/ Broome, Western Australia	—	A synonym of *N. belcheri*, herein
Nepanthia tenuis H. L. Clark, 1938 Broome, Western Australia	—	A synonym of *N. maculata*, herein
Parasterina occidentalis H. L. Clark, 1938 S.W. Australia	A synonym of *N. troughtoni*, A. M. Clark, 1966	As A. M. Clark, 1966
Nepanthia hadracantha A. M. Clark, 1966 Port Philip Bay, Victoria Australia	A synonym of *N. troughtoni*, Shepherd, 1968	As Shepherd, 1968
Nepanthia nigrobrunnea Rowe and Marsh/ Solitary Islands, New South Wales, Australia	—	New species herein
Nepanthia fisheri Rowe and Marsh Sabah, Indonesia	—	New species herein
Nepanthia gracilis Rowe and Marsh/ Philippines	—	New species herein

arms and "dorsal ossicles, especially those at the ends of the arms, broad rounded, the back covered with 2 or 3-beaked pedicellariae nearly hiding the tubercles". Perrier (1875) restricted the genus *Patiria* to the species *ocellifera* and *crassa*, relegating *coccinea* (the type-species of Gray's *Patiria*), *granifera* and *obtusa* to *Asterina*.

Fisher (1908), noted that Perrier had excluded the type-species, *P. coccinea,* from his genus *Patiria,* which is therefore not the *Patiria* of Gray, and renamed Perrier's genus *Parasterina,* with type-species *Patiria crassa*.

Verrill (1913), revised the subfamily Asterininae of the Asterinidae. He described several new genera and constructed a table (key) of genera and subgenera. He listed *N. maculata* as type-species of *Nepanthia* and included *brevis* in the genus. He included Fisher's *Parasterina* with type-species *crassa* and *P. obesa* H. L. Clark from Peru. The latter species has subsequently (Bernasconi 1973) been referred to *Patiria*. In his key Verrill allied *Parasterina* to his new genus *Allopatiria* with type-species *Patiria ocellifera* Gray, erroneously attributed to Australia by Verrill

Fisher (1940) doubted the validity of *Parasterina* after comparing a specimen of *P. crassa* (the type-species) with *Nepanthia variabilis* and *N. belcheri* and in 1941 used the combination *Nepanthia crassa*. H. L. Clark (1946), however, considered that *crassa, troughtoni* and *occidentalis* formed a homogeneous group easily distinguished from *Nepanthia* by having non-crescentic, crowded, often swollen abactinal plates and inconspicuous papulae; he referred the three species back to *Parasterina*.

Spencer and Wright (1966) include *Parasterina* in the synonymy of *Nepanthia*.

A. M. Clark (1971, in Clark & Rowe) indicated that some synonymisation of the tropical species of *Nepanthia* may be necessary when sufficient material has been examined.

After a study of most of the type-specimens of species referred to *Nepanthia* and collections housed in several Australian and international institutions, we have concluded that only 5 of the previously described species of *Nepanthia* warrant recognition, of these four occur around the coasts of Australia. Three new species are described, one each from north of Borneo, the Sulu Sea and New South Wales, Australia. Table 1 summaries the species referred to the genus *Nepanthia*.

ABBREVIATIONS

AM	The Australian Museum, Sydney, N.S.W. Australia.
BM	British Museum (Natural History), London, England.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
NMV	National Museum of Victoria, Melbourne, Victoria Australia.
USNM	United States National Museum (Smithsonian Institution), Washington D.C., USA.
WAM	Western Australian Museum, Perth, Western Australia.

SYSTEMATIC ACCOUNT

Family ASTERINIDAE

Genus **Nepanthia** Gray, 1840: 287

DIAGNOSIS: An asterinid genus with five or more distinct, elongate subcylindrical to tapering arms and a relatively small disc; abactinal surface strongly convex, actinal surface usually flat; adult size between 30 and 80 mm R. The abactinal plates appear crescentic to rhomboidal and are usually in distinct abactinal and lateral 'fields' on the arms; the primary plates imbricate throughout or only in certain areas, small secondary plates are often present. Marginal plates small, not prominent though they may delimit the lateral/actinal line. Actinal plates in 4-9 rows at base of rays, decreasing distally. Adambulacral plates bear a fan or comb of furrow spines backed by a fan or group of variously sized subambulacral spines which are sometimes larger than the furrow spines. All plates evenly covered or bearing tufts of spinelets which vary, between species, from short and thick set with many points to slender and hyaline with 1-3 points. Simple fasciculate pedicellariae are sometimes present. Several species fissiparous. Eight species recognised.

TYPE SPECIES: *N. maculata* Gray, 1840, restricted by Perrier, 1875, designated by Verrill, 1913.

OTHER SPECIES INCLUDED: *N. crassa* (Gray, 1847), *N. belcheri* (Perrier, 1875); *N. briareus* (Bell, 1894), *N. troughtoni* (Livingstone, 1934); *N. nigrobrunnea* n. sp., *N. fisheri* n. sp. and *N. gracilis* n. sp.

KEY TO SPECIES OF *NEPANTHIA*

1. Abactinal spinelets short, thick with many (more than eight) equal points; no prominent convex abactinal plates; distribution — southern Australia; two species ... 2

— Abactinal spinelets slender with few (not usually more than five) unequal points; one species *(crassa)* with spaced convex abactinal plates; distribution — Australia (except the south coast) and Indo-Malay region; six species ... 3

2. Exposed portion of plates of dorsal field rhomboidal, scarcely notched for papulae; 4-6 plates across the field at 1/2 R; papulae single; colour whitish-pink to deep rose, papulae red; southern Australia ... *N. troughtoni*

— Plates of dorsal field small, irregulary shaped, 8-10 plates across the field at 1/2 R; usually 2-3 papulae between plates; colour dark brown with black papulae; northern N.S.W. ... *N. nigrobrunnea*

3. Arms arched abactinally, actinal surface flat; marginal plates form a distinct actino-lateral edge ... 4

— Arms cylindrical or terete, marginal plates not forming a distinct actino-lateral edge . 5

4. Usually prominent convex primary abactinal plates with smaller secondary and granule-like tertiary plates between them; not fissiparous; colour usually mottled red/brown or brown, sometimes (at Abrolhos Is.) bright blue; west coast of Western Australia ... *N. crassa*

— Primary abactinal plates narrow, crescentic with small granule-like secondary plates around papulae; often fissiparous; mottled, variously coloured, often shades of grey or dull green or orange, red or brown; Indo-Malay region to northern Australia ... *N. belcheri*

5. Spinelets with 1-3 points ... 6

— Spinelets with more than 3 points ... 7

6. Arms terete, tapering to an acute tip; spinelets in 2-3 small tufts on the primary plates; colour (holotype) grey-blue; Philippines to Timor Sea .... *N. fisheri*

— Arms long, cylindrical or slightly tapering to a blunt tip; spinelets evenly covering primary plates; colour cream to buff, sometimes with dark spots; Philippines to northern Australia .... *N. maculata*

7. Five rays, not known to be fissiparous; cleaned abactinal plates flat; spinelets slender with 7-8 points; Philippine area and N.S.W. .... *N. gracilis*

— Multirayed, fissiparous; cleaned abactinal plates moderately convex; spinelets short with 5 or 6 points; South China sea to Moluccas .... *N. briareus*

Nepanthia troughtoni (Livingstone)
Figs 1; 2d, e; 5k; 6l.

Parasterina troughtoni Livingstone, 1934: 179, pl. 18 figs 1-6 — H. L. Clark, 1938: 180; 1946: 143.—Rowe and Pawson, 1977: 346.

Parasterina occidentalis H. L. Clark, 1938: 180, pl. 21 fig. 5; 1946: 143.—Rowe and Pawson 1977: 346.

Parasterina sp. c.f. *troughtoni*.—A.M. Clark, 1956: 378, text fig. 3, pl. 11.

Nepanthia hadracantha. A. M. Clark, 1966: 320, text fig. 3, pl. 3, figs 4-6.

Nepanthia troughtoni. A. M. Clark, 1966: 322.—Shepherd, 1968: 748.—Rowe and Pawson 1977: 348.

MATERIAL EXAMINED: 1 specimen (R/r = 16/4.5 mm = 3.5), holotype, *N. troughtoni*, AM No. J3978; 1 spec. (R/r = 34/7 mm = 4.8), paratype, *Parasterina occidentalis* AM No. J6178; 1 spec. (R/r = 67/12 mm = 5.6), paratype, *P. occidentalis* WAM 46-32; 1 spec. (R/r = 37/9 mm = 4.1), paratype, *P. occidentalis*, WAM No. 606-31; 1 spec. (R/r = 55/12 = 4.6), holotype, *N. hadracantha*, NMV No. H14.

In addition 77 specimens from the W.A. Museum, 7 specimens from the Australian Museum and 10 specimens from the S.A. Museum were examined. A summary of data for the 99 specimens examined is given in Table 2.

Table 2. Variation in size and R/r ratio of specimens of *N. troughtoni* from five areas of the coast of southern Australia.

Distribution	Number of Specimens	Max. R/r, mm.	Min. R/r, mm.	Range R/r	Mean R, mm.	Mode R, mm.
W.A. 30°05′S to 32°20′S	26	80/17	19/5	3.3-5.8	48.6	41-50
W.A. 33°10′S to 34°0′S	27	64/14	25/6	3.6-5.0	40.7	31-40
South Coast W.A.	28	65/11	16/4.5	3.5-5.9	47.7	41-50
South Australia	16	62/15	38/9	3.7-5.9	46.5	31-40
Victoria	2	57/11	55/12	4.6-5.2	—	—
	99	80/17	16/4.5	3.3-5.9	45.9	41-50

Table 3. Size distribution (R) of the specimens of *N. troughtoni* in 10 mm class intervals.

1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90
0	2	8	25	34	22	7	1	0

DIAGNOSIS: A species of *Nepanthia* with 5 cylindrical to slightly tapering blunt ended arms, non fissiparous. Maximum known R/r of 80/17 mm, mean R of 46 mm, range of R:r from 3.3 to 5.9; colour pinkish-white to rose with red papulae; abactinal plates rhomboidal, slightly convex; crystal bodies, secondary plates and pedicellariae absent; abactinal spinelets all over plates, short and stout with ca 10-20 points surrounding a prominent hemispherical to slightly pointed boss; furrow armature in overlapping combs of 4-5 subequal furrow spines with 6-10 subambulacrals in 2-3 rows; intertidal to 73 metres on rock, southern Australia.

COLOUR: *N. troughtoni* varies in colour from pinkish white-through salmon-pink to rose with red papulae and red skin visible between the plates in life.

HABITAT AND DISTRIBUTION: The habitat is on open coasts exposed to considerable wave action where it is found under reef ledges, grazing on encrusting organisms such as compound ascidians, under boulders or on vertical rock faces in the sublittoral. *N. troughtoni* is recorded from Wilsons Promontory, southern Victoria, around southern Australia to Green Head (30° 05' S) on the west coast of Western Australia. The known depth range is from the intertidal to 73 metres.

REMARKS: A. M. Clark (1966) referred *Parasterina troughtoni* to the genus *Nepanthia*, at the same time synonymising *P. occidentalis* with it and describing a new species, *N. hadracantha*. A. M. Clark (1966) also showed that there is quite a significant difference between the form of the spines of the cool temperate species *N. hadracantha* and its tropical congeners.

Shepherd (1968), after examining 47 specimens from Victoria and Western Australia, together with those collected during extensive underwater surveys of the coastal waters of South Australia, discussed the variation in arm taper, size and crowding of the abactinal plates and variation in the spinelets concluding that there was no evidence for maintaining *N. hadracantha* and synonymised it with *N. troughtoni*.

In comparing the holotypes of *N. troughtoni*, *N. occidentalis* and *N. hadracantha* the only detectable difference is in the slightly stouter, squatter shape of the spines of *N. occidentalis*, a difference not considered here of specific importance in view of Shepherd's (1968) observations.

Examination of a large series of specimens (99) shows considerable variation in the size of the abactinal plates and in the regularity of their arrangement. The specimens range in size from R/r = 16/4.5 mm (holotype of *N. troughtoni*) to 80/17 mm, while the R/r ratio varies from 3.3 to 5.9, the mean R measurement is 45.9 mm and the mode lies in the class interval 41-50 mm. The figures (Table 3) show a normal size distribution with a complete lack of very small specimens as with many other asteroids. No geographical differences can be detected in the size of specimens or in R/r ratios. There is considerable variation, however, in the length and breadth of arms within a population.

Nepanthia nigrobrunnea n. sp.
Figs 1; 2a, b, c; 5i; 6j, k.

MATERIAL EXAMINED: 1 specimen (R/r = 65/15 mm = 4.3) holotype, AM No. J10147, Groper I, Coffs Harbour, N.S.W., on reef, 20 m, N. Coleman, September, 1976; 3

specimens (R/r = 69-75/14.5-16 mm = 4.6) paratypes, AM No. J9885, Julian Rocks, Byron Bay, N.S.W., 10-30 m, S. Parish, May, 1976; 3 specimens (R/r = 56-66/13-14 mm = 4.3-4.7) paratypes, AM No. J9135 locality as J9885, on reef, 18 m, N. Coleman, 30.3.75; 2 specimens (R/r = 53-64/14-15 mm = 3.5-4.4) paratypes, AM No. J10920, Groper I, Coffs Harbour, N.S.W., 16 m, J. Ogg and C. Short, 19.8.77.

DIAGNOSIS: A species of *Nepanthia* with 5 subcylindrical to slightly tapering blunt ended arms, non fissiparous. Maximum known R/r of 75/16 mm, mean R of 62 mm, range of R:r from 4.3 to 5; colour dark brown with black papulae; abactinal plates somewhat irregular in shape, often double notched with 2-3 papulae (sometimes 1 or 4) to an area; crystal bodies, secondary plates and pedicellariae absent; abactinal spinelets all over plates, short and stout with 12-16 points, the central one sometimes enlarged; furrow spines in a comb of 3-4 subequal spines with 6-7 subambulacral spines in 2 rows; sublittoral, 10-30 metres, on rock, known only from northern N.S.W., Australia.

DESCRIPTION: The holotype has 5 arms, subcylindrical tapering evenly to a narrow but blunt tip; R/r = 65/15 mm = 4.3; br = 15.5 mm at base and 9 mm at two-thirds R. The madreporite is inconspicuous, lying in one interradius about 4 mm from the centre of the disc. The abactinal plates are all similar in size (about 1.1 mm maximum diameter). There are two 'fields' of plates, the dorsal field, where the order is irregular, and a lateral field each side, with the plates forming 10-11 longitudinal rows (at least proximally). The shape of the plates from the dorsal field is variable, from transversely elongate to triangular or rounded (fig. 5i). The proximal edge of the majority of plates is concave so that the plates can be said to be generally crescentic. Proximally there are about 3 plates between the lateral fields, 8-10 plates at half R and 6-7 plates at the arm tip. The plates of the lateral fields are more regularly triangularly crescentic. The first row extends to the arm tip, the succeeding rows extending to shorter distances so that the 11th row comprises only 3-4 plates at the arm base.

The actino-lateral edge is rounded. The inferomarginal plates form a regular row of longitudinal plates (about 1.7 mm x 0.7 mm proximally) along the arm, becoming shorter, rounded and convex distally. The superomarginals are smaller than the inferomarginals and from the 12th-14th inferomarginal there are 2 small superomarginal plates aligned per inferomarginal. The superomarginals are irregular distally, and difficult to distinguish. The adambulacral plates bear 3-4 subequal, flat-tipped furrow spines backed by six or seven subambulacral spines arranged in 2 rows. The first actino-lateral row of plates extends almost to the arm tip. The second row comprises 7-8 plates, the third row 3-4 plates and 3-4 plates are present in the distal triangle of the actinal surface. The oral plates bear 5 furrow spines and 7-8 suboral spines. The proximalmost suboral spine is largest. The spinelets on the abactinal and actinal plates are spaced and coarse. Abactinally the largest plates bear up to 45 spines, the actinal plates bear about half of this number. The abactinal spinelets are 2.5-3 times as long as their maximum width (base) and some have a median, large, blunt process between the terminal points (fig. 6j, k). The spinelets are remarkably even in size (360-375 μm long x 120-150 μm wide). The actinal spines are larger, 2.7-2.8 times as long as wide (570-600 μm long x 200-240 μm wide) (fig. 2c).

Between the plates of the dorsal field are 1-4, usually 2-3, papular pores but between the plates of the lateral fields only 1 pore per plate occurs. There are no pores between the plates of the 10-11th rows of lateral plates or actinally. There are no fasciculate pedicellariae. Besides the holotype, there are eight paratypes which are similar in all respects to the holotype.

COLOUR: In life the animal is very dark brown, with black papulae.

HABITAT AND DISTRIBUTION: Known from Byron Bay to the Solitary Islands, New South Wales, Australia, in 10-30 m depth.

ETYMOLOGY: *nigrobrunnea* (Lat.) refers to the colour of the animal.

REMARKS: *N. nigrobrunnea* is most closely allied to the Flindersian species *N. troughtoni* from which it is most easily distinguished by the arrangement of marginal plates, the shape of plates in the dorsal field, groups of 2-4 papulae and colour. These features alone would distinguish *nigrobrunnea* from its tropical congeners but additionally the shape of the spines covering the skeletal plates distinguish this species and *troughtoni* from the tropical species.

The closer relationship of *nigrobrunnea* with the Flindersian species would indicate that though this species occurs in the northern parts of New South Wales (where there is a known overlap of tropical and warm temperate species) it can be considered a Peronian species. Its presently known restricted distribution is difficult to assess though a somewhat similar situation occurs on the western coast of Australia where *Nepanthia crassa* occupies the whole west coast. It might be expected that *nigrobrunnea* will be found further south along the New South Wales coast. Whether *nigrobrunnea* is derived from Flindersian stock is difficult to determine. It might be speculated that *troughtoni* and *nigrobrunnea* have developed independently from the progression of a northern species southward along either side of the continent. However, the form of *nigrobrunnea* compares much more closely with that of the Flindersian *troughtoni* than its tropical congeners *belcheri* and *maculata*. That *nigrobrunnea* has developed after a possible isolation from *troughtoni* due to the separation of populations by the Bassian isthmus during the Pleistocene epoch is possibly more likely than a development from the small, highly fissiparous *belcheri* from the north.

Nepanthia crassa (Gray)
Figs 1; 3a, b, c; 5g, j; 6d, e.

Patiria? crassa Gray, 1847: 83; 1866: 17.

Patiria crassa. — Perrier, 1875: 326-327.

Parasterina crassa. — Fisher, 1908: 90; 1940: 270-271. — H. L. Clark, 1923: 243; 1938: 179-180; 1946: 143.

Nepanthia crassa. — Fisher, 1941: 451-455, figs 20, 21, pl. 70, fig. 2.

non Patiria crassa. — Bell, 1884: 131. — Whitelegge, 1889: 201.

MATERIAL EXAMINED: See Table 4 for a summary of data for the 127 specimens examined from the Australian and Western Australian Museums.

DIAGNOSIS: A species of *Nepanthia* with 5 subcylindrical to slightly tapering, stout, blunt ended arms. Maximum known R of 72 17 mm, mean R of 40 mm, range of R:r from 2.8 to 5.1; colour variable, unicolorous blue, blue-green or orange, more often mottled browns or pink to red and brown; papulae single; primary abactinal plates subcrescentic, imbricating when young, tumid to hemispherical, surrounded by numerous secondary plates when large; few crystal bodies on plate margins; fasciculate pedicellariae usually on plates of the lateral field; thorny abactinal spinelets with 5-8 points cover primary plates and occur in tufts on secondary plates; furrow spines in a graduated fan of 7-10 (usually 9) spines with a fan of 7-10 subambulacral spines and 5-7 spinelets; intertidal to 38 metres, on rock, sand and muddy sand, on the west coast of Western Australia, from Point Cloates to Cape Naturaliste.

COLOUR: In colour *N. crassa* is variable, usually brownish, sometimes mottled with darker shades; a specimen from Shark Bay was pinkish-buff, mottled with red-brown and dark brown while at the Abrolhos Islands most specimens are blue or blue-green.

Table 4. Variation in size and R/r ratio of specimens of *N. crassa* from four areas in Western Australia.

Distribution (Western Australia)	Number of specimens	Max. R/r, mm.	Min. R/r, mm.	Range, R/r	Mean, R, mm.	Mode, R, mm.
22°40′S to 29°55′S	23	60/14	23/7	3.1-4.6	38.0	31-40
Abrolhos, 28-29°S	45	72/17	18/6	2.8-4.4	38.1	31-40
Fremantle area, 32°S	52	65/15	15/5	3.0-5.1	42.2	41-50
Geographe Bay, 33°35′S	7	56/14	34/9	3.7-4.7	43.6	41-50
	127	72/17	15/5	2.8-5.1	40.5	31-40

Table 5. Size distribution (R) of the specimens of *N. crassa* in 10 mm class intervals.

1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90
0	4	24	44	38	16	3	1	0

HABITAT AND DISTRIBUTION: *N. crassa* is found in sheltered bays, commonly under jetties and on piles but is also found on sand amongst seagrass, mud or amongst algal covered rocks. In the Abrolhos *N. crassa* occurs near islands on the western platforms e.g. around Gun Island (Pelsaert group), Rat I. (Easter Group) and Pigeon I. (Wallabi group) in areas protected by seaward reefs from much wave action. The substrate is rock with a thin covering of algae and silty sand. During the day the animals are concealed in crevices or under dead coral slabs and are active at night on the reef platform. They are rarely found elsewhere in the Abrolhos. *N. crassa* is confined to the west coast of Western Australia between Cape Naturaliste (33°35′S) and the Point Cloates area (22°40′S) where it is separated by North West Cape from populations of *N. belcheri* and *N. maculata* in Exmouth Gulf. The recorded depth range is from the intertidal to 38 metres.

REMARKS: The history of generic changes undergone by this endemic Western Australian species are given in Table 1.

Fisher (1940, 1941) re-described *N. crassa*, showing (1941, figs 20, 21) the imbrication of the abactinal plates, thus removing the main character by which his genus *Parasterina* was distinguished from *Nepanthia*. H. L. Clark (1946) stressed the shape of the abactinal plates as characterising *Parasterina crassa*, *troughtoni* and *occidentalis*. Since the latter two species have already been included in *Nepanthia* (A. M. Clark, 1966) and the shape of the plates does not differ significantly in small specimens of *crassa*, H. L. Clark's view cannot be upheld.

In small specimens of *N. crassa*, e.g. WAM 54-79, which has R/r of 30/9 mm, (fig. 5j), the abactinal plates imbricate regularly and are notched for papulae; they are slightly tumid with secondary plates only around the papular pores and few tertiary plates in the dorsal field. The plates of the lateral field also imbricate regularly but most lack secondary plates. A large specimen, WAM. 625-75 with R/r of 57/15 mm, (fig. 5g), has the primary abactinal plates

widely separated, linked by secondary plates with numerous small tertiary plates in the dorsal field and 2-5 small plates around the papulae of the lateral field. In this specimen the primary plates are not greatly enlarged nor very tumid but a few examples e.g. WAM. 756-75, (fig. 3a), the primary plates are almost hemispherical, on short stout arms. The abactinal and actinal plates are covered in a dense coat of thorny spinelets which radiate from the small secondary and tertiary plates but give an even coating to the primary plates. Detail of the abactinal spinelets is shown in figure 6d, e; they most closely resemble those of *N. belcheri*. The furrow armature, actinal surface and pedicellariae all closely resemble *N. belcheri*, pointing to a close relationship of the two species. The fact that both Bell (1884) and Whitelegge (1889) identified specimens of *N. belcheri*, from the east coast of Australia, as *N. crassa*, highlights the resemblance of the two species. The principal difference is in the shape of the abactinal plates, crescentic in *N. belcheri*, very convex and rounded or irregular in shape in adult *N. crassa*, and in the presence of tertiary as well as secondary plates in *N. crassa*.

Among the specimens examined the arms vary in shape from slightly tapering to quite cylindrical, apart from a slight ventro-lateral angle, but are always blunt ended. The majority of specimens have moderately convex primary plates and slightly tapering arms.

The variation in size of specimens from four areas on the Western Australian coast (Table 4) shows a geographical trend with higher mean and modal sizes (R) in specimens from the southern part of the range (Fremantle to Cape Naturaliste). Measurements of the 127 specimens as a whole, however, show a similar trend to that shown in *N. troughtoni*, but with a slightly lower mean R measurement, 40.5 mm, the mode falling in the class interval 31-40 mm (Table 5), there being a similar lack of very small specimens.

Nepanthia belcheri (Perrier)

Figs. 1; 3d, e; 5a, b; 6a, b.

Asterina (Nepanthia) belcheri Perrier, 1875: 320.

Asterina belcheri. — Bell, 1884: 131.

Asterina (Nepanthia) brevis Perrier, 1875: 321. — Bell, 1884: 131, pl. 8, figs A, a. — Studer, 1884: 41.

Nepanthia suffarcinata Sladen, 1888: 328, pl. 28, figs. 9-12. — Koehler, 1910a: 133; 1910b: 288. — Clark and Rowe, 1971: 38 (distribution), 66 (key).

Nepanthia belcheri. — Sladen, 1889: 387. — H. L. Clark, 1938: 169; 1946: 141. — Kenny, 1969: 51, figs. 1-4. — Endean, 1953: 54; 1956: 125; 1957: 240; 1961: 291. — Clark and Rowe, 1971: 38 (distribution), 66 (key). — Otteson, 1976.

Nephanthia brevis. — Sladen, 1889: 387, pl. 63, figs 3-5 — Döderlein 1896: 40. — H. L. Clark, 1921: 95, pl. 6, figs 3-4 (col.); 1938: 172; 1946: 141. — Endean, 1953: 54; 1956: 125; 1957: 240; 1965: 230. — Clark and Rowe, 1971: 38 (distribution), 66 (key).

Patiria crassa. — Bell, 1884: 131. — Whitelegge, 1889: 201 (*non P. crassa* Gray).

Nepanthia joubini Koehler, 1908: 232, figs 1-4. — Fisher, 1919: 423, pl. 113, figs 1-2. — H. L. Clark, 1938: 172 (footnote). — Clark and Rowe, 1971: 38 (distribution), 66 (key). — Domantay, 1972: 55.

Henricia heteractis H. L. Clark, 1909: 530, pl. 49, figs 1-2; 1926:2.

Nepanthia polyplax Döderlein, 1926: 20, pl. 4 figs 2-2a.

Nepanthia ? brevis. — Livingstone, 1932: 262, pl. 5, figs 8-9.

Nepanthia magnispina H. L. Clark, 1938: 174, pl. 20, figs 1-2; 1946: 142.

Nepanthia variabilis H. L. Clark, 1938: 176, pl. 10, figs 4-5 (col.), pl. 20, figs 4-5; 1946: 141. — Fisher, 1941: 454, fig. 22. — Clark and Rowe, 1971: 38 (distribution), 66 (key).

MATERIAL EXAMINED: 1 specimen (R/r = 15/3.8 mm = 3.9) holotype of *N. belcheri*, BM No. 1847.3.10.4; 1 specimen (R/r = 24/5.7 mm = 4.2) holotype of *N. brevis*, BM 1854.11.15.290; 1 specimen (R/r = 25/8 mm = 3.1) holotype of *Henricia heteractis*, AM No. G11430; 1 specimen (R/r = 31.9/8.5 mm = 3.8) holotype of *N. magnispina*, MCZ No. 3230; 2 specimens (R/r = 30-50/6.7-10 mm = 4.5-5.0) paratypes of *N. variabilis*, MCZ No. 3225; 2 specimens (R/r = 40-47/10-11 mm = 3.6-4.7) paratypes of *N. variabilis*, WAM No. 119-39, 120-39; 4 specimens (R/r = 32-62.5/7.5-12.5 mm = 4.3-5.3) paratypes of *N. variabilis*, AM No. J6187.

In addition 138 specimens from the Western Australian and Australan Museums were examined. A summary of data for the 150 specimens is given in Table 6.

DIAGNOSIS: A fissiparous species of *Nepanthia* with 4-7 (usually 5-6) subcylindrical to slightly tapering, moderately stout arms. Maximum known R/r of 65/14 mm, mean R of 31 mm, range of R:r from 2.0 to 5.3; colour highly variable, often grey-green or fawn ground colour mottled with red, green, brown or black; papulae single, lying in notch of abactinal plates which have a raised crescentic ridge carrying spinelets, with crystal bodies on the lower parts of the plates; fasciculate pedicellariae usually present on plates of the lateral field; abactinal spinelets, with 3-5 acute points, on ridges of primary plates and on 2-4 secondary plates, adjacent to the papulae; furrow spines in a graduated fan, usually 8-9, with a subambulacral fan of 7-12 spines and 3-7 additional spinelets; intertidal to 46 metres on a muddy sand and rock substrate, Burma to northern Australia.

COLOUR: Highly variable, often grey-green or fawn ground colour mottled with red, green, brown or black.

HABITAT AND DISTRIBUTION: *N. belcheri* is found from the intertidal to a known depth of 46 metres. Near low tide mark it may be found clinging to the underside of boulders on a muddy sand or rock substrate. The species appears to be always associated with somewhat muddy conditions. Geographically *N. belcheri* ranges from the tropical coast of Australia, northwards to the Philippines, Cochin China (Vietnam) and west to Burma.

REMARKS: Although he was convinced that his species *Henricia heteractis* from Lord Howe Island and Döderlein's *Nepanthia polyplax* from Rockhampton, Queensland, were conspecific with *Nepanthia belcheri*, H. L. Clark (1938) described two new species *N. magnispina* and *N. variabilis* from north-western Australia.

The similarity of specimens of *N. variabilis* and *N. brevis* led the present authors separately to question the basis for separating them and a comparison with specimens of *N. belcheri* indicated that this species could not be distinguished morphologically from the other two species. The results of an examination of 150 specimens of the three nominal species, ranging from Lord Howe Island and Port Jackson, N.S.W. through Queensland and Torres Strait to Exmouth Gulf, Western Australia, including the holotypes of *N. belcheri*, *N. brevis*, *H. heteractis* and *N. magnispina* and eight paratypes of *N. variabilis*, are presented in Table 6. It is evident that two of the key characters used by Clark (1938) to separate *N. belcheri*, *N. brevis* and *N. variabilis* i.e. the number of arms and number of furrow spines, do not provide a basis for distinguishing them. Samples from the three areas, east coast of Australia, Torres Strait to Darwin and north western Australia (Table 6), corresponding to the distribution of the three nominal species

Table 6. Variation in *Nepanthia belcheri*.

	Number of specimens		
	East coast and Lord Howe I,	Torres Strait to Darwin	Kimberley to Exmouth Gulf
Size R in mm			
1-10	8	1	0
11-20	22	3	3
21-30	17	11	12
31-40	11	25	10
41-50	2	4	15
51-60	0	0	3
61-70	0	1	2
	N = 60	45	45
	Mean 22.2	33.4	38.1
	Mode 11-20	31-40	41-50
Number of Furrow spines			
5-6	6	0	0
6-7	16	0	2
7-8	13	12	11
8-9	19	22	17
9-10	5	6	5
10-11	0	6	6
	N = 59	45	41
	Mean 7.5	8.8	8.5
	Mode 8-9	8-9	8-9
Number per plate, Abactinal spines			
<30	8	1	0
31-40	35	5	5
41-50	13	17	3
51-60	1	12	13
61-70	1	5	7
71-80	0	4	8
>81	1	0	7
	N = 59	44	43
	Mean 38.15	51.25	61.56
	Mode 31-40	41-50	51-60
Number of arms			
4	0	1	2
5	21	38	39
6	28	3	4
7	11	3	0

	N = 60	45	45
	Mean 5.8	5.2	5.0
	Mode 6	5	5
R/r ratio			
Max. R/r	46.5/15.0	63.0/13.5	65.0/14.0
Min. R/r	8.0/3.0	10.0/3.0	12.0/4.0
Range R/r	2.0-5.0	2.8-4.4	3.0-5.3

Table 7. Percentage of specimens of *N. belcheri* with various arm numbers.

	N	< 5	5	6	7	> 7
Moreton Bay (Kenny, 1969)	837	10	8	55	25	1
Townsville (Otteson, pers. comm.)	613	22	<2	25	44	<6
East Coast Queensland	60	0	35	47	18	0
Torres Strait to Darwin	45	2	84	7	7	0
Kimberley to Exmouth Gulf	45	4	87	9	0	0

respectively, show close similarity in the number of furrow spines, all having a modal number of 8-9. The slightly lower mean number in the east coast population is related to the smaller mean and modal R measurements of these specimens.

The mean and modal size of specimens increases progressively northwards and westwards, with a corresponding decrease in fissiparity. The sample of the east coast population is 65% multibrachiate and 35% five rayed, the north coast sample is 13% multibrachiate and 84% five rayed and the northwest sample is 9% multibrachiate and 87% five rayed. A few specimens from northern Australia and the northwest are four rayed.

A comparison of the arm numbers of specimens from Moreton Bay, Townsville and the present, smaller, sample from the whole east coast of Queensland (Table 7) shows a preponderance of 6 rayed specimens in Moreton Bay and on the east coast overall while 7 rayed specimens predominate at Townsville. A much higher proportion of 5 rayed specimens occur in the present sample from the Queensland coast than in the other two studies. The reason for the preponderance of small fissiparous specimens in the east coast population is unknown. Kenny (1969) showed that members of the Moreton Bay population of *N. belcheri* reproduce asexually by fission in their second or third year. Otteson (1976), studying the reproductive pattern of *N. belcheri*, found the Townsville population to be serially protandric hermaphrodites in which sexual reproduction appeared to be modified by fissiparity.

A parallel to the east coast population of small sized fissiparous *N. belcheri* is found in *Coscinasterias acutispina* Stimpson, where a dwarf race, reproducing fissiparously was reported from the island of Maui, Hawaii while normal specimens were found in Kaneohe Bay, Oahu, Hawaii (Edmondson, 1935). Edmondson also referred to a small fissiparous *Nepanthia?* sp. However, one of us (F.W.E.R.) has re-examined this specimen and found it to represent *Asterina burtoni* Gray.

Clark's third distinguishing character, the shape of the abactinal plates, varies within each population and is not a reliable distinguishing character. The number of spinelets per abactinal

plate also varies within each population, but since it is related to the size of the specimen, the number is higher in the populations of larger individuals from north and northwestern Australia (Table 6). The shape of the abactinal spinelets is identical in the three populations (Figs 6a, b).

The type locality of *N. belcheri* is uncertain though Bell (1884) recorded specimens from Port Jackson, N.S.W. and there are three specimens in The Australian Museum and one in the Stockholm Museum from Lane Cove River, Port Jackson, N.S.W. These were reported by Whitelegge (1889) as *Patiria crassa,* redetermined by H. L. Clark as *Henricia heteractis* (1926) and later as *Nepanthia belcheri* (1938). No other records of this species exist from New South Wales. A. M. Clark (pers. comm.) has thoroughly researched the literature and found that the type locality for the species could not be New South Wales since Belcher did not visit Australia on his voyages. His specimens were more likely to be from Indonesia. Its occurrence in the Moluccas is confirmed by Koehler (1910a), as *N. suffarcinata* (2 five rayed specimens taken from 15 m in Aru) and by specimens recorded here from 25-45 m in the Aru Islands.

Nepanthia joubini was described from Cap St. Jacques, Cochin China (Vung Tau, Vietnam). Both Fisher (1919) and Clark (1938) doubted the validity of *N. joubini,* Fisher considering it to be probably conspecific with *N. brevis* and Clark with *N. belcheri.* A. M. Clark (in Clark and Rowe, 1971) also noted that *N. joubini* would probably prove to be conspecific with *N. belcheri.* Livingstone (1932) identified a specimen of *N. belcheri,* with 6 rays and 5 madreporites, from the vicinity of Low Islands, North Queensland as *N. brevis,* remarking on the resemblance to Fisher's example of *N. joubini.*

A. M. Clark (1971) also indicated that *N. suffarcinata* might be conspecific with *brevis* or *variabilis.* In comparing Sladen's (1888) description of *N. suffarcinata,* collected from Burma, with our data, we consider the species to be conspecific with *N. variabilis* or *N. brevis,* and therefore falling within the range of *N. belcheri.* Examination of the holotype of *N. magnispina* by one of us (F.W.E.R.) shows it to be virtually identical with specimens of *N. belcheri* from Queensland and New South Wales. There is evidence of a third regenerating arm (H. L. Clark notes only 2), a small madreporite is present (H. L. Clark missed it) and the number of spines on the abactinal plates and adambulacral plates is similar to the specimens of *N. belcheri* collected from Lane Cove River, N.S.W. The "enlarged oral spine" recorded by H. L. Clark, is not particularly prominent and falls certainly within the range of variation of sizes of spines seen within the 150 specimens examined.

This study has led to the conclusion that *N. brevis, N. suffarcinata, N. joubini, N. magnispina* and *N. variabilis* should be regarded as junior synonyms of *N. belcheri,* a somewhat variable species occurring on the east, north and northwest coasts of Australia from Lord Howe Island and southern Queensland to Exmouth Gulf and in Indonesia, the Philippines, Vietnam and Burma.

Nepanthia fisheri n. sp.

Figs 1; 4a, b, c; 5d, h; 6g.

Nepanthia maculata. — Fisher, 1919: 423 (part) (non *N. maculata* Gray).

MATERIAL EXAMINED: 2 specimens, the holotype, WAM 102-78, and paratype WAM 101-78, from west Banguey channel, northeast of Sabah, dredged on mud, 25 fms (46 m), B. R. Wilson on 'Pele', 11.III.1964; 1 specimen WAM 42-69 from 8 km west of Agal Bay, N.W. Sabah, dredged on mud, 16 fms (29 m), B. R. Wilson on 'Pele', 12.III.1964; 1 specimen WAM 100-78, from 14 km west of Cape Melville, Balabac I., Philippines, dredged on sand, 27 fms (49 m), B. R. Wilson on 'Pele', 9.III. 1964; 2 specimens, USNM40290 & 40371, from Linapacan Strait, N. of Palawan I., Philippines, 11° 37' 15" N: 119° 48' 45" E, Albatross st. 5335, 46 fms (84 m) sand, mud, 18.XII.1908 (included in *N. maculata* by Fisher, 1919); 1 specimen AM

J12649, from st. 1154, 11° 48' S: 129° 19' E, 68 m (Timor Sea), R. Martin (CSIRO).

DIAGNOSIS: A species of *Nepanthia* with 5 regular, strongly tapering arms, not known to be fissiparous. Maximum known R/r of 40/9.5 mm, mean R of 19 mm, range of R:r from 3.4 to 4.1; colour of holotype blue-grey; abactinal plates broadly crescentic slightly notched for single papulae with 2-3 raised areas bearing spinelets separated by lower areas with crystal bodies; 1-2 secondary plates usually occur in the papulae areas; abactinal spinelets in radiating groups of short sharp single pointed spinelets on the raised areas of each plate and on the secondary plates; furrow spines in a graduated fan of 8 with a fan of 8 subambulacral spines and 10-15 additional spinelets; sublittoral on mud or sand, 29-84 metres, Philippines to the Timor Sea.

DESCRIPTION: The holotype has 5 subequal tapering arms, R/r 38-40/9.5 mm = 4.1, br 9-10 mm at base of ray decreasing to 5 mm at half R and 2.5 mm just proximal to the terminal plate; R/br at base 4.1. Rays elongate, broad at the base, tapering to a narrow tip. Abactinal surface of the disc and rays convex, depressed interradially, interbrachial arcs acute; actinal surface plane but margin of disc and rays not distinct. There are two madreporites both situated nearer the centre of the disc then the margin, one is radial in position, 2 mm in diameter, the other interradial and 1.5 mm in diameter. The anus is central, surrounded by about 8 small granules.

The abactinal spinelets are in radiating groups arising from 2 or 3 raised areas on each plate, giving the impression of a large number of small convex plates. The imbricating abactinal plates are arranged in dorsal and lateral fields; when denuded the exposed part of the plates of the dorsal field are seen to be broadly crescentic, 1 to 1.2 mm in diameter on the proximal part of the arm, and slightly notched for single papulae, beside which are two small rounded supplementary plates. Secondary plates are absent distally. Plates of the dorsal field are fairly regularly arranged with alternating transverse rows of plates across the ray. There are 6 plates in a diagonal series across the dorsal field at half R. Plates of the dorsal field have 2-3 raised areas separated by lower areas with embedded crystal bodies. Each raised area bears a radiating group of 20-25 short, sharp spinelets, tapering to a single point while each secondary plate has a group of 5-10 similar spinelets, fig. 6g.

The lateral field of plates is in six longitudinal rows at the base of the ray decreasing to three at half R. Two rows extend to the arm end. The terminal plate is rounded, 1 mm in diameter.

The spinelets of the lateral arm plates are arranged in a horseshoe shape proximally giving the impression that they surround a pedicellaria pit but no modified or enlarged spinelets are present, nor are pits present on the denuded plates.

Superomarginal plates, small and rounded, alternate with elongate, angled inferomarginals; occasionally small supplementary plates lie between the superomarginals. The proximal end of each inferomarginal slightly overlaps the distal end of the preceding one; they project very slightly, scarcely forming an angled margin to the rays. Interradially they are less conspicuous and tend to lie on the actinal surface. Spinelets on the marginals are similar to those of the abactinal plates, about 20 on each superomarginal and 40 to each inferomarginal, proximally.

Actinal plates in 4 series at base of rays with an extra plate or two interradially in some arm angles. The innermost row of squarish plates, each opposite a similar adambulacral plate extends nearly to the arm end; distally they become compressed and similar in shape to the inferomarginals; the second row extends to about half R, with odd plates extending further; the third row extends to between one third and half R or to about the 15th inferomarginal; the fourth row extends to the 5th inferomarginal and three interradial plates represent a fifth series of actinal plates. The convex actinal plates are closely covered by about 50 radiating, short,

pointed, glassy spinelets.

Adambulacral plates bear a webbed fan of 8 graduated furrow spines, of which the central one is up to 1 mm in length, followed by a webbed fan of 8 slightly smaller, blunt subambulacral spines while 10-15 tapering, pointed spinelets cover the remainder of the plate; these spinelets are considerably thicker than those of the adjacent actinal plates (fig. 4c).

Oral plates have a similar armature to the adambulacrals each with a marginal series of 8 spines, of which the innermost pair are longer and stouter than the remainder; there are 6-7 suboral spines, of which the last two are very small and 10-14 smaller thorny spinelets on the actinal surface of the plates.

The paratype (WAM 101-78) has five equal rays and one madreporite, R/r = 20/5.5 mm = 3.6, br = 5.5 mm at base of ray, 4 mm at half R (Fig. 4b).

The specimen is similar to the holotype although little more than half the size. The arms are less attenuated, there are 4 instead of 6 series of plates in the lateral field at the base of the rays and fewer papulae; secondary abactinal plates are few and scattered. The innermost row of actinal plates extends nearly to the arm end, the second row varies between the 7th to 12th inferomarginal, the third row extends to the 2nd or 3rd inferomarginal and the fourth is represented by 1-3 plates in the arm angle. The furrow and oral spines are as described for the holotype.

OTHER SPECIMENS: Among the other specimens, WAM 42-69 has five equal rays and a single madreporite, R/r = 18/5 mm = 3.6, br = 5.5 mm at base of ray, 4 mm at half R. This specimen differs from WAM 101-78 only in having the plates of the dorsal field on the rays less distinctly subdivided. WAM 100-78 has six rays, two of 11 mm R and four of 8 mm, r = 3 mm, R/r = 3.7, br at base = 3 mm, 2.5 mm at half R. There are two madreporites. The characteristic features of the species are less developed in this small specimen but it resembles the larger specimens more closely than it does *N. belcheri*.

The characteristic appearance of the abactinal plates, their surface subdivided and bearing tufts of spinelets is progressively less clearly seen in the smaller specimens and is scarcely distinguishable in the smallest.

One specimen (AM J12649), from the Timor Sea, has five unequal rays, two of 27.5 mm, two of 26.5 mm and one of 12 mm, r = 5-7 mm, R/r = 2-3.5, br at base = 7 mm, 4 mm at half R. There are 2 madreporites. The appearance of the abactinal plates is characteristic. However, there are often 3 secondary plates proximal to the crescentic abactinal plates.

Two small specimens (USNM 40290 and 40371) from the Philippines were doubtfully referred by Fisher (1919, p. 423) to *N. maculata*. These are both five rayed with a single madreporite and anus and have R/r of 12/3.5 mm and 15/4 mm. Fisher noted that "A peculiarity of these two specimens is the grouping of spinelets of the abactinal crescentic plates in 3 or sometimes 2 distinct tufts to each plate. This gives the appearance of numerous small plates. These small specimens are distinct from *N. brevis* and *N. suffarcinata*, and of course may represent a third species. Their affinities are close to *N. maculata*".

These two specimens have been examined and are here referred to *N. fisheri*. Had Fisher seen a larger specimen he would have been in no doubt that they represented an undescribed species. Fisher's specimens agree closely with the holotype and other specimens examined.

COLOUR: Uniform blue-grey with madreporites cream in life.

HABITAT AND DISTRIBUTION: The holotype and paratypes were all taken in the area north of Sabah, Borneo, dredged on mud or sand at 29-49 metres. Fisher's specimens were taken

north of Palawan Island, Philippines, on sand and mud at 84 metres.

ETYMOLOGY: The species is named in honour of W. K. Fisher.

REMARKS: *Nepanthia fisheri* has affinities with both *N. belcheri* and *N. maculata* but has a very distinct facies of its own. It differs from *N. maculata* in having tapered arms and in the character of the abactinal plates which bear tufts of spinelets on two or three raised areas on each plate in contrast to the uniform covering of spinelets on each plate in *N. maculata*. Like *N. maculata* the pointed spinelets are in radiating groups but are shorter and less numerous in *N. fisheri*.

The similarity in general form of the small specimens to those of *N. belcheri* points to the close relationship between the two species. *N. fisheri* has crystal bodies embedded in the skeletal plates, as in *N. belcheri*. The adambulacral armature of *N. fisheri* differs little from either species. The fact that one specimen is six rayed and that the holotype has two madreporites indicates that the species is potentially fissiparous although the other specimens are five rayed with a single madreporite.

The most distinctive feature of *N. fisheri*, apart from the shape, is the grouping of the short, sharp glassy spinelets on several raised areas on each abactinal plate. A comparison with *N. gracilis* n. sp. is made under the latter species.

Nepanthia maculata Gray
Figs 1; 2f; 5e; 6h,i.

Nepanthia maculata Gray, 1840: 287; 1866: 15. — Studer, 1884: 42. — Sladen, 1889: 388, pl. 64, figs 1-4. — Fisher, 1919: 422, pl. 113, figs 3, 4. — A. M. Clark, 1956: 377, text fig. 2. — Clark and Rowe, 1971: 38 (distribution), 66 (key). — Domantay, 1972:55.

Chaetaster cylindratus Mobius, 1859: 3, pl. I, figs 3, 4.

Asterina (Nepanthia) maculata.— Perrier, 1875: 322.

Nepanthia tenuis H. L. Clark, 1938: 175, pl. 20, fig. 3; 1946: 142.— Clark and Rowe, 1971: 38 (distribution), 66 (key).— Rowe and Pawson, 1977: 347.

MATERIAL EXAMINED: 1 specimen (R/r = 38.6/6.8 mm = 5.7) holotype of *N. maculata*, BM No. 1953. 4.27.40, Migupou, Philippines 7-12 fms (2-5.5 m), fine sand, coral; 1 specimen (R/r = 38.5/5.5 mm = 7) paratype of *N. tenuis*, AM No. J6176, Broome, Western Australia; 2 specimens (R/r = 94/15 and 83/10 mm), Darwin Museum, off Weipa, Gulf of Carpentaria; 1 specimen (R/r = 75/11 mm) Darwin Museum, off Christmas Creek, Gulf of Carpentaria, 14°30'S: 141°30'E; 1 specimen (R/r = 72/13 mm), Darwin Museum off Tasman Pt., Gulf of Carpentaria; 1 specimen (R/r = 47/8 mm), Exmouth Gulf, W.A., WAM 1825-75, coll. J. Penn on 'Flinders' 1.VIII.1975, trawled 9-20 m; 1 specimen (R/r = 50-70/13 mm), 6 km west of Dampier, W.A., WAM 587-75 coll. L. Marsh, 28.X.1972, on muddy sand flat, exposed at low spring tide; 2 specimens (R/r = 50/7 mm and 35/6.5 mm), N.E. of Malus I., Dampier Archipelago, W.A., Mariel King Exped., 31.V.1960, WAM 586-75, dredged on sandy rubble, 18 m; 2 specimens (R/r = 38/6 mm and 23/4 mm) 11-16 km W.N.W. of Cape Melville light, Balabec I., Philippines, WAM 585-75, coll. B. R. Wilson on 'Pele', 9.III.1964, dredged on coarse sand, 37-49 m; 1 specimen (R/r = 44/6 mm) off Elat Bay, west coast of Nuhu Tjut, Kai Is., Indonesia, st. KN II, 5°40'S: 132°59'E, WAM 57-79, M. King Mem. Exped., 13.VI.1970, dredged on sand and rubble, 49-84 m; 1 specimen (R/r = 31/4 mm) north of Du Rowa I., Kai Is., Indonesia, st. KR VI/1, 5°32'S: 132°41'E, M. King Mem. Exped., 10.VI.1970, dredged on sand, 33-37 m; 1 specimen (7 rays, R/r = 18-28/r mm) off Tg Tutuhuhur, Piru Bay, Ceram, st. CPI 1-6, 3°15'S: 128°8'E, M. King Mem. Exped., 1.VI.1970, dredged on coarse sand, 42-64 m.

DIAGNOSIS: A species of *Nepanthia* usually with 5 regular, subcylindrical arms, non fissiparous. Maximum known R/r of 94/15 mm, mean R of 51 mm, range of R:r from 5.4 to 8.3; colour cream to buff unicolorous or with the central disc area dark blue, brown or green with a few flecks of the same colour on the arms; abactinal plates broadly crescentic to rhomboidal, notched for single papulae and often pitted for pedicellariae, a few crystal bodies on plate margins, often absent; fasciculate pedicellariae, when present, in the dorsal field; secondary plates few, usually absent; abactinal spinelets slender, tapering with 1-3 (rarely 4) acute points, all over plates; furrow spines in a graduated fan of 7-8 with a fan of 9-12 subambulacrals and 9-12 additional spinelets; intertidal to 84 metres, on muddy to coarse sand with rubble or coral, Philippines to northern Australia.

COLOUR: Specimens from the Philippines and Indonesia vary in colour from cream with a large dark blue to violet spot on the disc centre and small spots on the arms to mottled light orange and cream with a few dark brown spots on the arms or light brown with a dark brown spot in the centre of the disc and small brown spots on the arms. Northern Australian specimens are either uniformly cream or buff with or without dark brown spots. The holotype of *N. tenuis* was light grey with scattered flecks of deep green.

HABITAT AND DISTRIBUTION: *N. maculata* is a rather uncommon species found on mud, sand or sand and rubble bottoms from the intertidal to at least 84 metres. Studer's record of a specimen of R/10 mm from 400 fms (731 m), McCluer Gulf, New Guinea is questionable since the maximum chart depth in the Gulf is 56 fms (102 m) although deep water (to 1000 fms) is found between the Gulf and Ceram. *N. maculata* is known from the Philippines, Moluccas and northern Australia, from the Gulf of Carpentaria to Exmouth Gulf, Western Australia.

REMARKS: A. M. Clark (in Clark & Rowe, 1971) commented that *N. tenuis* might prove to be a synonym of *N. maculata*. Direct comparison of the holotype of *N. maculata* and a paratype of *N. tenuis* shows them to be conspecific, neither possessing secondary abactinal plates, and both being similar in size. The presence of secondary plates may well be related to size of the animal since large specimens from northern Australia (Gulf of Carpentaria and northwestern Australia) possess scattered secondary plates. The other characters (R/r ratio and number of furrow spines) used in H. L. Clark's 1938 key do not provide distinguishing features, since the R/r ratio of one of the paratypes of *N. tenuis* is identical to that of the holotype of *N. maculata*. Likewise, although the holotype of *N. tenuis* has 5-6 furrow spines, a paratype has 7-8.

The R/r ratio of specimens of *N. maculata* examined varies from 5.8 to 7.8 in those from the Philippines and Indonesia and from 5.5 to 8.3 in those from northern Australia. There are 8 furrow spines in the specimens from the Philippines and Indonesia, 7 to 8 in those from northern Australia. We can see no valid reason, therefore, for not considering *N. tenuis* and *N. maculata* to be conspecific. Pedicellariae, not previously described in *N. maculata*, occur on some of the northern Australian specimens, usually on the dorsal field of arm plates with a few on the disc and lateral field of arm plates. The fasciculate pedicellariae consist of 4-7 stout, thorny, tapering spinelets surrounding a furrow on the plate just distal to the papular pore.

Nepanthia gracilis n. sp.

Figs 1; 4d, e, f; 5f; 6f.

MATERIAL EXAMINED: Two specimens, the holotype, WAM 103-78 from 14 km and 242° from Zal I., S.W. of Pearl Bank, Sulu Sea, Philippines, dredged from 122-124 m, heavy sponge, B. R. Wilson on 'Pele', 22.XI.1964 and the paratype WAM 104-78, from 15 km and 242° from Zal I., S.W. of Pearl Bank, Sulu Sea, dredged from 100 to 110 m, heavy sponge, B. R. Wilson on 'Pele', 22.XI.1964; two specimens (R/r of 65/14 and 57/12 mm) trawled off Crowdy Head, N.S.W., 31°59'S: 152°57'E to 31°56'S: 152°58'E, 'Kapala' st. 78.05.08, 110 m, AM No.

J11880.

DIAGNOSIS: A species of *Nepanthia* with 5 regular strongly tapering arms, non fissiparous. Maximum known R/r of 65/14 mm, mean R of 49 mm, range of R:r from 4.6 to 5.3; colour unknown, cream when dry; abactinal plates triangular to rhomboidal, flat except for bosses for spinelets, sometimes a few crystal bodies on plate margins; single papulae; no secondary plates; abactinal spinelets subcylindrical, with thorny tips (7-8 acute points), all over plate; furrow spines in a comb of 4-5 subequal spines and 6-7 shorter subambulacral spines sometimes arranged in two rows; sublittoral, 100-124 metres, with sponges; Philippines and eastern Australia.

DESCRIPTION: The holotype has 5 equal tapering arms, R/r = 37/7 mm = 5.3, br = 7 mm at base of ray decreasing to 4 mm at half R and 1.5 mm just proximal to the terminal plate (Fig. 4d, e, f).

Rays elongate, pointed, tapering from the base to a very narrow tip. Abactinal surface of the disc and rays convex, depressed interradially; interbrachial arcs acute; actinal surface plane but margin of disc and rays not distinctly angled. The single madereporite is interradial in position, nearer the margin than the centre of the disc. The anus is central, concealed amongst the disc spinelets.

The skeletal plates are covered in slender spinelets standing vertically, not radiating. Arm skeleton composed of dorsal and lateral fields of imbricating plates; the exposed portion of those of the dorsal field varies in shape from broadly crescentic to rounded or squarish, often irregular in outline; surface of plates flat except for minute bosses for spinelet attachment; few crystal bodies. The plates are scarcely notched for single papulae; secondary plates absent (fig. 5f). There are 3 plates across the dorsal field at base of ray, 6 in a diagonal series at about half R; near the arm end dorsal and lateral fields not clearly distinguished. At the base of the ray there are 10 rows of triagnular to squarish plates in the lateral field, decreasing to 6 at half R; distally the series are no longer differentiated from the dorsal field but on some rays one row extends to the arm end.

Papulae occur singly between all plates of the dorsal and lateral fields except near the arm tip and in the arm angle.

Plates of the dorsal field bear 25-35 slender, more or less cylindrical spinelets with thorny tips (fig. 6f) while those of the lateral field have 15-20 similar spinelets, near the base of the ray, decreasing in number distally. No pedicellariae.

Superomarginal plates large and rounded, more prominent than inferomarginals, usually lying opposite them, occasionally alternating; inferomarginals elongate, angled, proximal end of one overlapping the distal end of the preceding one; inferomarginals lie entirely on the actinal surface of the rays so that the superomarginals form the ventrolateral margin of the arms and disc although not forming a conspicuous angle; spinelets on marginals similar to those on abactinals, about 20 per superomarginal and 16 per inferomarginal.

Actinal plates in 5 rows, with 1 or 2 plates of a 6th row, at base of ray; innermost row extends to 0.8 R (5 mm from arm tip), second row to nearly half R or the 18th inferomarginal, third row to 9th or 10th inferomarginal, fourth row to 4th inferomarginal, with 1 or 2 plates in the arm angle representing a 6th row. The actinal plates are moderately convex and carry 5-10 slender thorny tipped spinelets standing vertically.

Adambulacrals usually bear 4 (3-5) elongate cylindrical furrow spines, up to 1 mm in length, the middle two slightly longer than the others; 6-7 similar but shorter subambulacral spines, sometimes arranged in two rows. Oral plates each have a marginal series of 6 spines decreasing in size from the innermost towards the furrow and 7 elongate suboral spinelets.

The paratype (WAM 104-78) has R r of 37 7 mm 5.3, br 7 mm. It is identical to the holotype except for the presence of 2 small secondary plates in the dorsal field on one ray and the furrow spines are more frequently in combs of 5 rather than 4.

OTHER SPECIMENS: Two specimens from N.S.W. are provisionally referred to this species. They are badly distorted and not well preserved but agree in most respects with the description of *N. gracilis*. The abactinal plates of the dorsal field are less regular in shape and arrangement, and are more numerous than in the holotype or paratype but near the ends of the arms the cleaned plates match those of the holotype very closely. At the base of the ray there are 8 rows of actinal plates in the N.S.W. specimens compared with 5 6 in the holotype of *N. gracilis*. These differences could well be attributable to the larger size of the N.S.W. specimens. The abactinal and actinal spinelets and the furrow spines agree closely with *N. gracilis*. The specimens are referred to *N. gracilis* with some hesitation but they are not sufficiently distinctive to describe as new; further specimens should clarify the position. They were taken at the same depth as the Philippines specimens and the occurrence of *N. gracilis* at 31 S is not impossible.

COLOUR: Not recorded in life, but dry it is cream.

HABITAT AND DISTRIBUTION: This species is known only from the two specimens described above, both taken with sponges from 100 to 124 m near Pearl bank in the Sulu Sea and two specimens provisionally referred to this species, from 110 m, off N.S.W., Australia.

ETYMOLOGY: The species is named from the Latin *gracilis* in reference to the slender, tapering arms.

REMARKS: *N. gracilis* resembles *N. fisheri* in size and form but closer examination shows them to be very different. The disc of *N. gracilis* is smaller and the rays more slender than those of *N. fisheri* but the most distinctive difference is in the nature of the spinelets which are cylindrical and slender, standing more or less vertically in *N. gracilis* in contrast to the short, tapering acutely pointed spinelets radiating from 2-3 elevations on each abactinal plate in *N. fisheri*. Crystal bodies are present in *N. fisheri*, absent in *N. gracilis*. Papulae extend further into the lateral field in *N. gracilis* than in *N. fisheri* and there are more rows of lateral plates in *N. gracilis*. The superomarginals are more prominent than the inferomarginals in *N. gracilis* while the reverse is true of *N. fisheri*. The furrow spines are in combs of 4-5 spines of nearly equal length in *N. gracilis* in contrast to the fans of 8 graduated spines in *N. fisheri*.

N. gracilis is most nearly related to *N. briareus* from which it differs in being non fissiparous and in the form and covering of the abactinal plates.

In *N. briareus* the plates tend to be crescentic particularly on the proximal part of the arms and spinelets are borne on the convex ridge of each plate. The proximal plates of *N. gracilis* are not convex or crescentic and tend to be rhomboidal or irregular in shape. The disc plates of *N. briareus* are smaller than the dorsal arm plates and irregular in shape, in *N. gracilis* they tend to be larger than the dorsal arm plates. The dorsal field of plates is more distinctly set off from the lateral field in *N. gracilis* than in *N. briareus*. The arrangement of marginal and actinal plates is similar in both species.

The abactinal spinelets of both species are shown in figs 6f and 6e. The sponelets of *N. gracilis* are longer than those of *N. briareus*, with up to eight acute points in contrast to up to six rather blunt points in *N. briareus*.

Nepanthia briareus (Bell)
Figs 1; 4g; 5e; 6e.

Patiria briareus Bell, 1894: 404, pl. 25, figs 1-3.

Nepanthia briareus.— A. M. Clark, 1956: 374-377, text fig. 1, pl. 10.— Jangoux, 1978: 297-298.

MATERIAL EXAMINED: 1 specimen, lectotype, Macclesfield Bank, South China Sea, 55 to 83 m. BM No. 1892. 8.22.267, 7 rays, (3 long, R = c. 35 mm, 4 short, R = 17-20 mm, r = 6.5 mm, R/r = 5.4); 1 specimen from Taluk Dodinga, Halmahera, Indonesia, st. Hd 1/4-5, 0°49'N: 127°31'E, M. King Mem. Exped., 20.V.1970, dredged with sponge and alcyonarians, 82 m, 7 rays, (3 long, R = 29 mm, 4 small, R = 17-20 mm, r = 6 mm, R/r = 5.0), 3 madreporites; 2 specimens, off Elat Bay, West coast Nuhu Tjut, Kai Is, Indonesia, st. KN II, 5°40'S: 132°59'E, M. King Mem. Exped., 13.VI.1970, dredged on sand and rubble, 27-46 m, 7 rays, (4 long , R = 36-44 mm, 3 small, R = 25-26 mm, r = 9 mm, R/r = 5.0), 2 madreporites; and 7 rays, (3 long, R = 30 mm and 4 smaller, R = 25-26 mm, r = 7 mm, R/r = 4.3), 2 madreporites, WAM 56-79.

DIAGNOSIS: A fissiparous species of *Nepanthia* with 7-10 (usually 7) slender, terete arms. Maximum known R/r of 44/9 mm, mean R of 34.4 mm, range of R:r from 4.3 to 5.4; colour uncertain, one specimen faded orange after drying from formalin; papulae single; abactinal plates oval, diamond shaped or irregular tending to have an oval or crescentic ridge bearing short thorny spinelets with 5-6 blunt points; no secondary plates, no crystal bodies; furrow spines in a comb of 4-5 with an oblique comb of 5 subambulacral spines followed by 1-4 spinelets. Found on sand and rubble sometimes with sponges and Alcyonaria; sublittoral, known depth range 27-83 m, South China Sea and Indonesia.

COLOUR: The colour of the three Indonesian specimens (after drying from formalin) is pale orange.

HABITAT AND DISTRIBUTION: This apparently uncommon species is known only from the South China Sea, Philippines (Jangoux, 1978) and the Moluccas, at a depth of [illegible] to 83 metres.

REMARKS: A. M. Clark (1956) redescribed the eight specimens collected from Macclesfield Bank (South China Sea) and selected a lectotype. Re-examination of the lectotype by one of us (F.W.E.R.) has revealed it to possess three small madreporites and two anal openings, indicating fissiparity, as suggested by A. M. Clark from observation of regenerating multibrachiate specimens in the British Museum (Natural History).

The specimens examined here (figs 4g, 5c) agree closely with the lectotype. Detail of the spinelets is shown in figure 6c.

N. briareus appears to be more closely related to *N. gracilis* n. sp. than to *N. maculata*, the differences are shown in the key.

DISCUSSION

The genus *Nepanthia* traverses the Indo-Malay Australian region extending from Mergui Archipelago (Burma) eastwards to the Philippine Islands and southwards through Indonesia to circumscribe Australia (fig. 1). Altogether 17 species have been described and referred at one time or another to the genus *Nepanthia*, either as valid species or as synonyms of those species (Table 1). In this study the number of previously described species has been further reduced, by synonymy, to five and three new species are described. *Nepanthia tenuis* is considered conspecific with *maculata* while *suffarcinata*, *brevis*, *joubini*, *variabilis* and *magnispina* are considered to be conspecific with *belcheri*. The synonymy of *belcheri* was realised after a study of 150 specimens ranging from New South Wales northward through Queensland and Torres Strait to Exmouth Gulf in Western Australia. Specimens vary in size from R of 8 mm to 65 mm and show a geographical cline from southern Queensland (?N.S.W.) to Exmouth Gulf (W.A.) with size and, concomitantly, spinulation increasing and fissiparity decreasing in that direction.

Both fissiparous and five rayed specimens have been recorded from Aru Is in the Moluccas (Koehler, 1910a and present study), fissiparous specimens from Vietnam (Koehler, 1908) and the Philippines (Fisher, 1919) and five rayed specimens from Burma (Sladen, 1888). Fissiparity appears to become predominant as a method of reproduction in response to certain ecological conditions, as yet undetermined.

The origin of the genus may well have been in the Indo-Malay region from where it extended to the southern coast of Australia. Ekman (1953) has pointed out that a high proportion of species and genera of the southern Australian fauna is of tropical origin. He also concluded that Australia had a basically northern (tropical subtropical) fauna and southern (warm-temperate temperate) fauna. H. L. Clark (1946) found that the distribution of echinoderm species corresponded fairly well with Hedley's (1904, 1926) four zoogeographical provinces, the Dampierian (Torres Strait to Geraldton on the west coast), Solanderian (Torres Strait to 26°S, on the Queensland coast), Peronian (south east coast) and Flindersian (southern and south western coasts). Clark ignored the Banksian province proposed by Whitley (1932) for the Queensland coastal fauna as distinct from the 'Solanderian' reef fauna. Wilson and Gillett (1971) prefer to divide the Australian molluscan fauna simply into northern and southern regions with a long overlap zone on the east and west coasts. The distribution of species of *Nepanthia* around Australia is therefore most interesting as it appears to support both of these views. That there is a northern and southern fauna is demonstrated by the *belcheri maculata* versus *troughtoni nigrobrunnea* distribution, with a distinctive difference in the more hyaline spinulation of the northern species compared with the coarse spinulation of the southern species. These species, on present known distribution, can be further assigned to zoogeographical provinces with *belcheri* extending across the Dampierian Banksian regions, *maculata* being Dampierian in Australian distribution, *troughtoni* Flindersian and *nigrobrunnea* Peronian. *N. crassa* occupies the western overlap zone. Wilsons Promontory, Cape York and North West Cape all provide sharp dividing lines (?barriers) between the distribution of *Nepanthia* species. North West Cape separates populations of *N. maculata* and *N. belcheri* from *N. crassa*. Cape York is the other end of the Australian range of *N. maculata* and Wilsons Promontory marks the eastern limit of *N. troughtoni*. It is curious that, if both *N. maculata* and *N. belcheri* originated in the Indo-Malay region, *N. belcheri* has spread through Torres Strait and far down the east coast of Australia, while *N. maculata* is only found west of Cape York despite the fact that their habitat requirements appear to be identical and they occur together in north Western Australia.

Neither species extends beyond Exmouth Gulf, which is the last suitable embayment until Shark Bay 500 km south of North West Cape is reached. However, *Nepanthia crassa*, which appears to be closely related to *N. belcheri*, replaces the latter on the western side of North West Cape extending from Point Cloates southwards to Cape Naturaliste, wherever suitable habitats occur.

Most of the *Nepanthia* species are found in sheltered, sometimes muddy, situations from shore to the inner continental shelf perhaps explaining why they have not spread far into the Indian and Pacific Oceans. They are what Endean (1957) has termed "mainland" rather than "reef" species.

N. troughtoni and *N. nigrobrunnea* differ from the other species in habitat requirements since they are both open coast species favouring rocky substrates exposed to considerable wave action.

N. belcheri has a floating yolky egg suggesting pelagic lecithotrophic development but the larval life span is unknown (Otteson, 1976). Nothing is know of the reproduction of the other species.

Further study of the ecological/physiological factors responsible for the predominance of

fissiparity over sexual reproduction in some populations of *N. belcheri* should be rewarding

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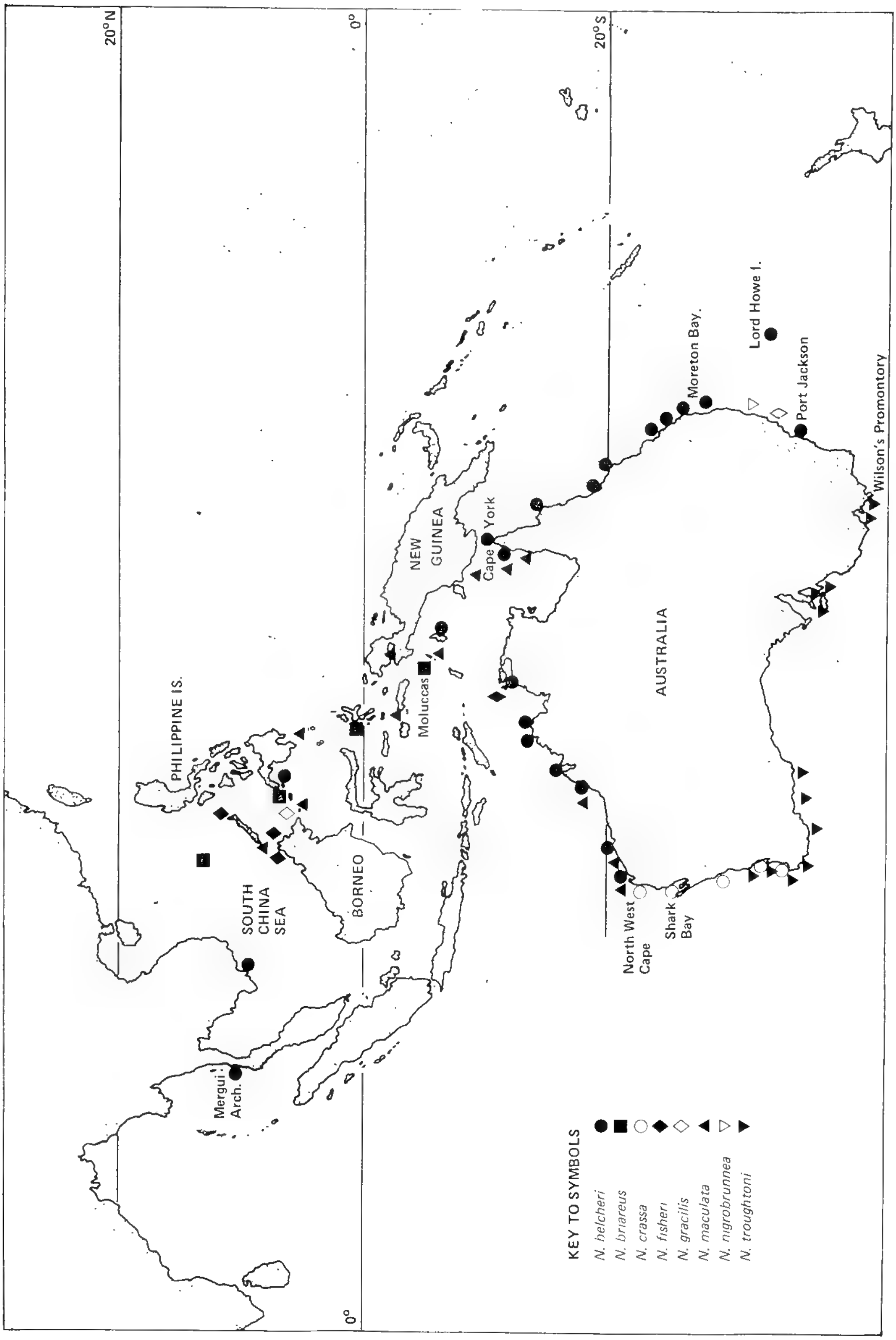

Fig. 1. Distribution of species of *Nepanthia*.

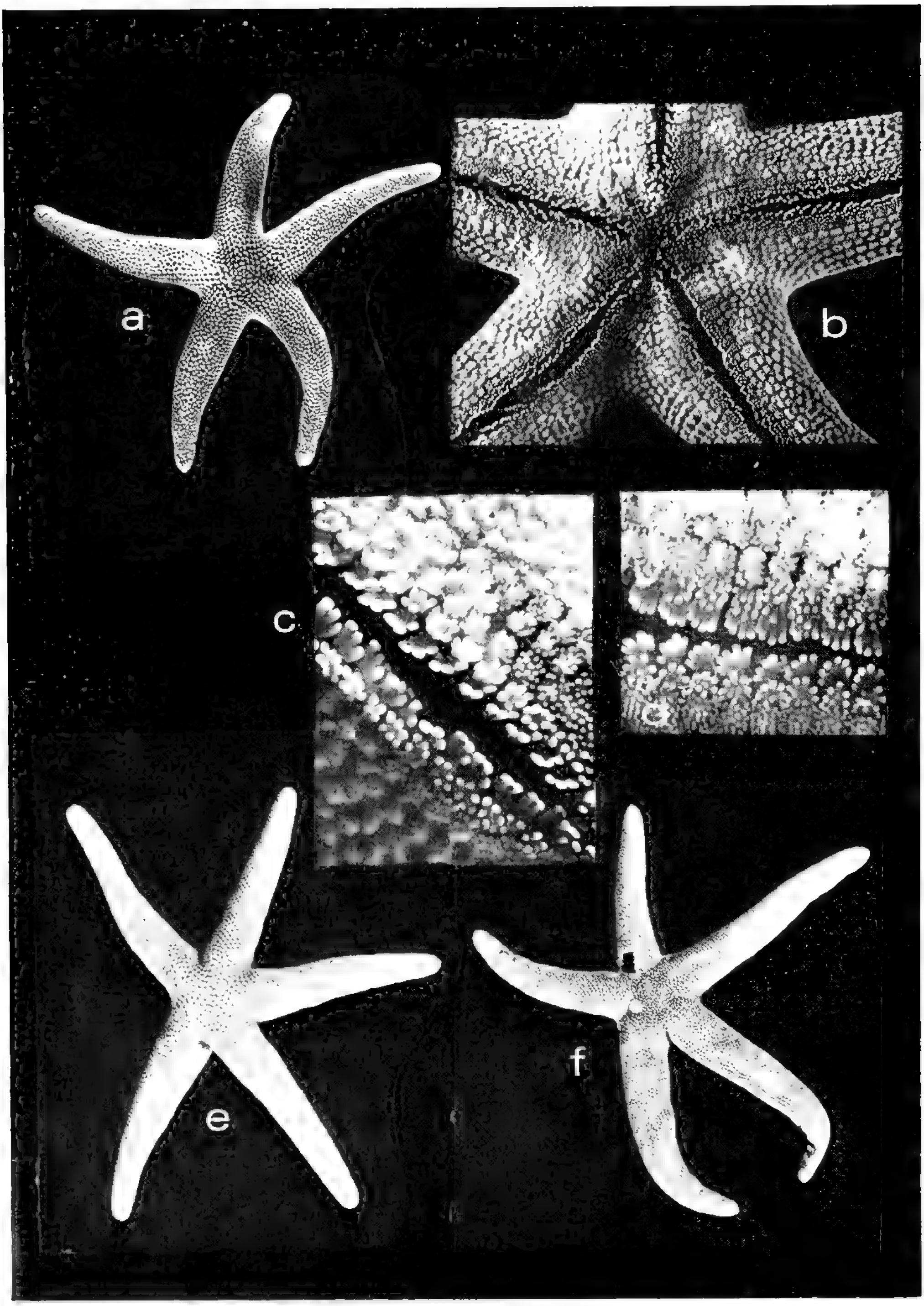

Fig. 2. a-c, *Nepanthia nigrobrunnea* sp. nov., holotype, **a**. abactinal, **b**. actinal, **c**. adambulacral armature, R/r = 65/15 mm; d-e, *N. troughtoni*, WAM 55-79 **d**. adambulacral armature, **e**. abactinal, R/r = 70/14 mm; **f**. *N. maculata*, WAM 587-75, abactinal, R/r = 70/13 mm.

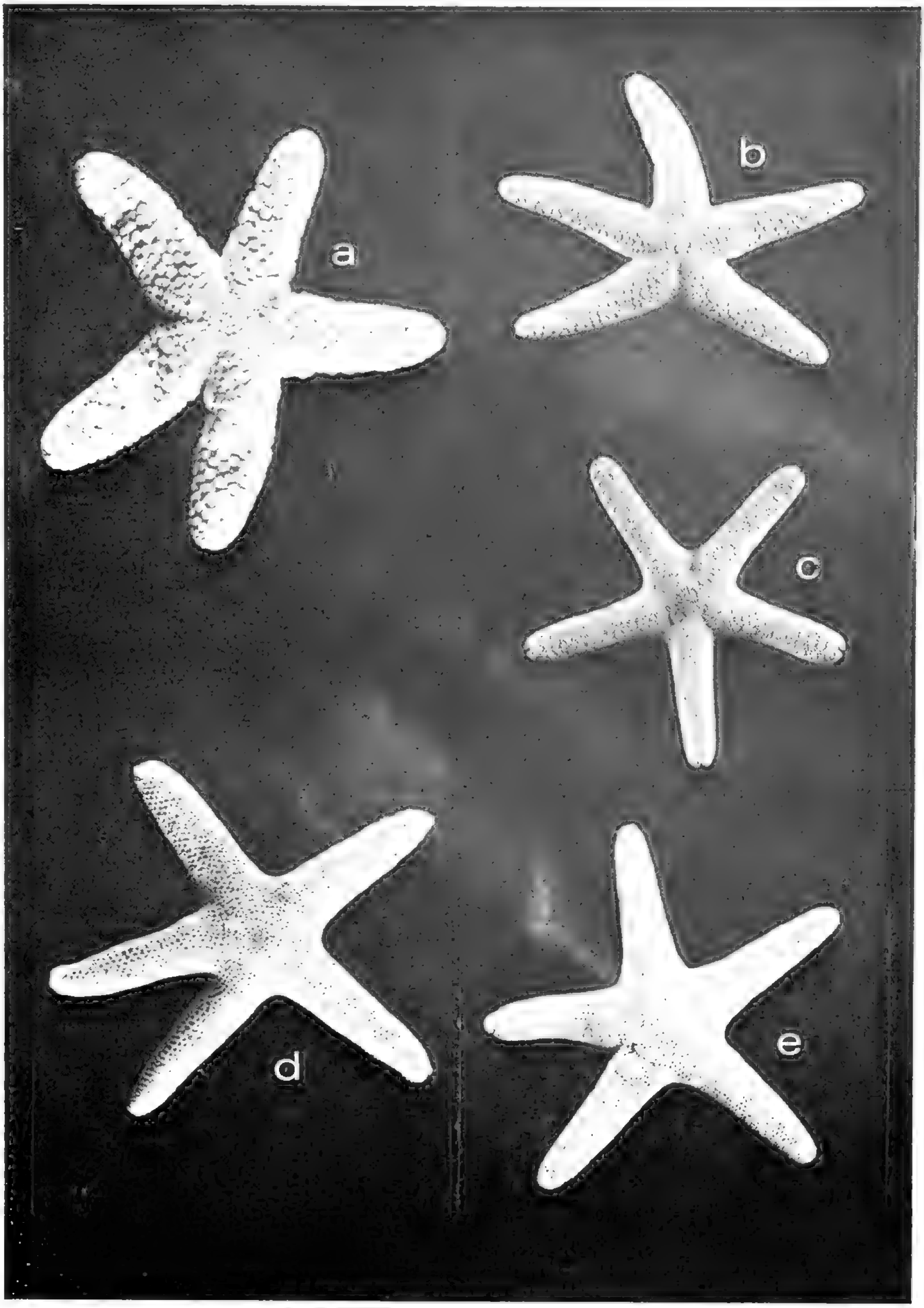

Fig. 3. a-c, *Nepanthia crassa*, **a.** WAM 756-75, abactinal, R/r = 43/13 mm; **b.** WAM 12-77, abactinal, R/r = 42/10 mm; **c.** WAM 607-75, abactinal, R/r = 37/10 mm; d-e, *N. belcheri*, **d.** WAM 590-75; Dampier, W.A., abactinal, R/r = 43/12 mm; **e.** WAM 615-77, Thursday Island, Qld., abactinal, R/r = 40/11 mm.

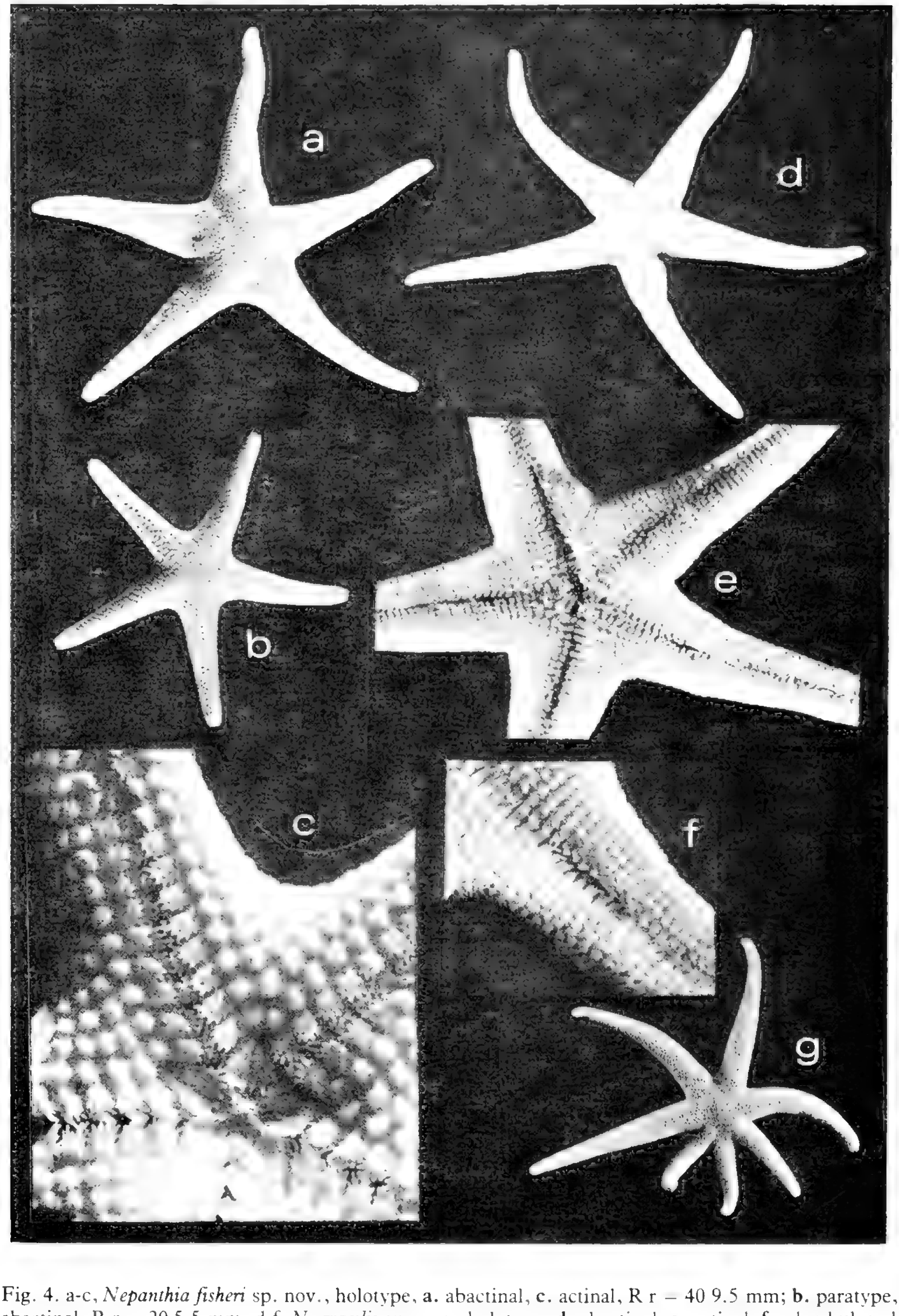

Fig. 4. a-c, *Nepanthia fisheri* sp. nov., holotype, **a.** abactinal, **c.** actinal, R/r = 40/9.5 mm; **b.** paratype, abactinal, R/r = 20.5/5.5 mm, d-f, *N. gracilis* sp. nov., holotype, **d.** abactinal, **e.** actinal, **f.** adambulacral armature, R/r = 37/7 mm; **g.** *N. briareus*, WAM 56-79, abactinal, R/r = 44/9 mm.

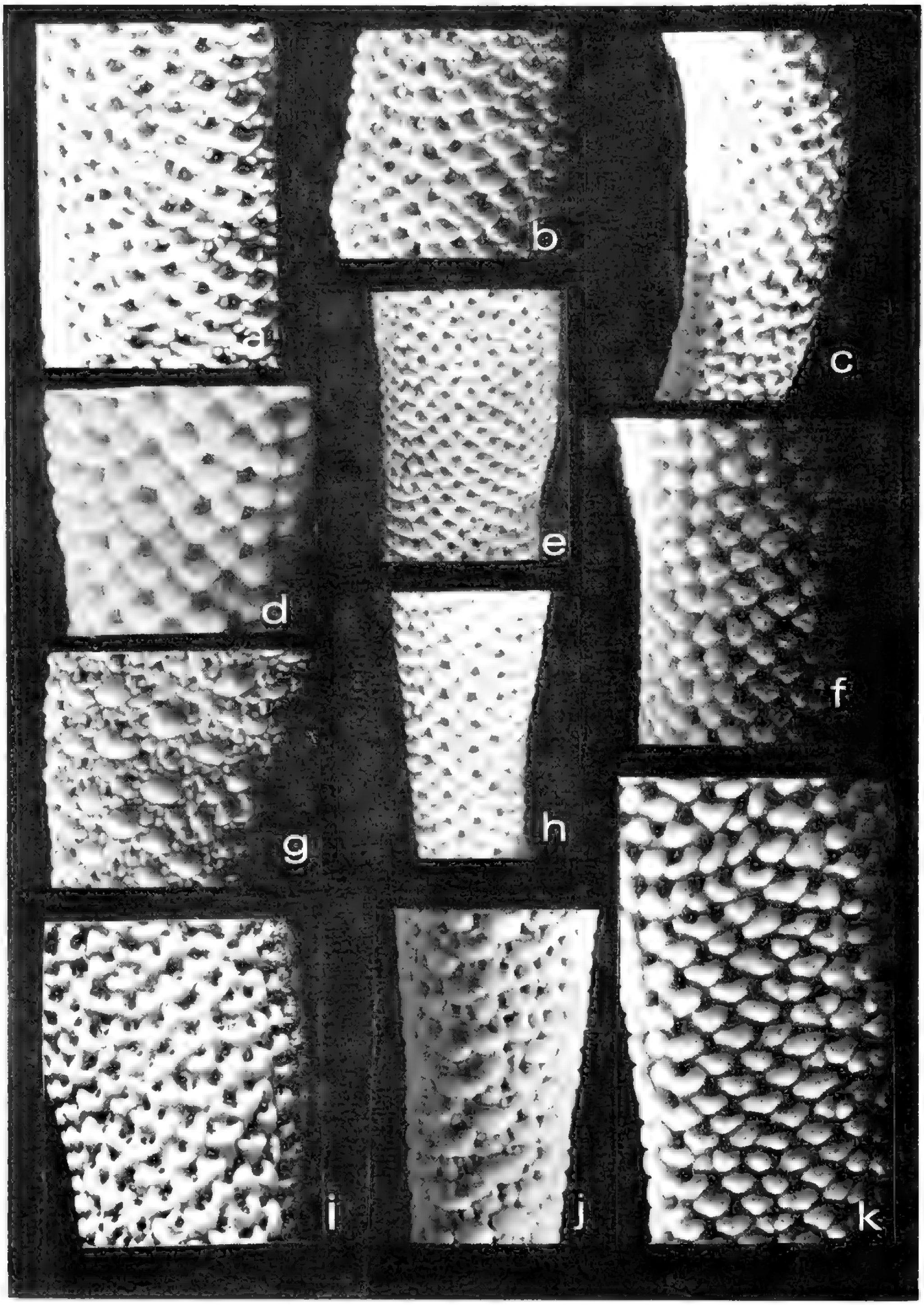

Fig. 5. Denuded arms of *Nepanthia* species. a-b, *N. belcheri*, **a.** WAM 615-77, Thursday I., Qld., R/r = 40/11 mm, **b.** WAM 296-75, Dampier, W.A., R/r = 41/12 mm; **c.** *N. briareus*, WAM 56-79, Moluccas, R/r = 44/9 mm; **d,h.** *N. fisheri* sp. nov., holotype, Sabah, R/r = 40/9.5 mm; **e.** *N. maculata*, WAM 1825-75, Dampier, W.A. R/r = 70/13 mm; **f.** *N. gracilis* sp. nov., holotype, Philippines, R/r = 37/7 mm; **g,j.** *N. crassa*, **g.** WAM 625-75 Cockburn Sound, W.A., R/r = 57/15 mm; **j.** WAM 54-79 Houtman Abrolhos, W.A. R/r = 30/9 mm; **i.** *N. nigrobrunnea* sp. nov., holotype, N.S.W., R/r = 65/15 mm; **k.** *N. troughtoni*, WAM 1486-74, Sorretono, W.A., R/r = 52/13 mm.

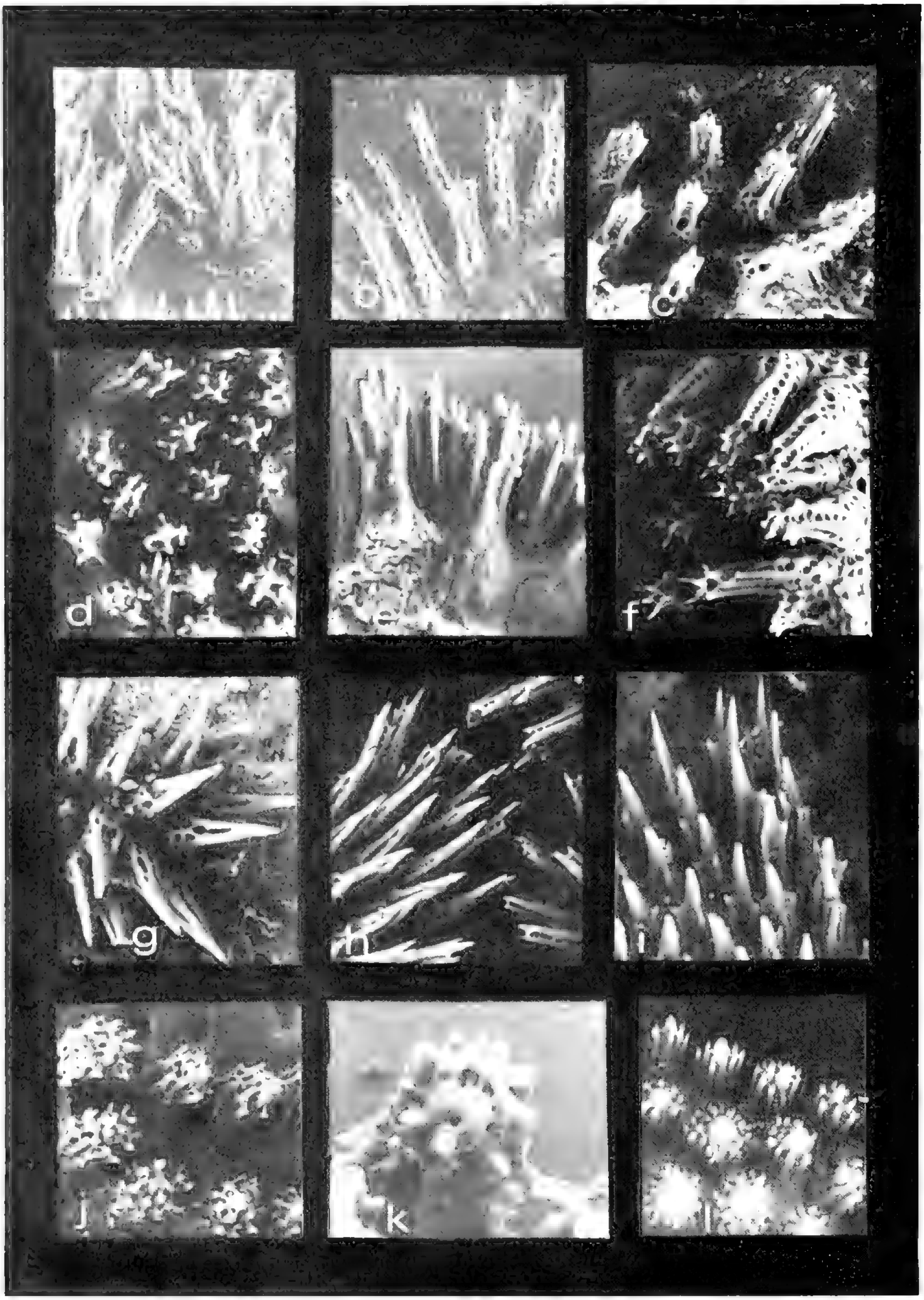

Fig. 6. Scanning electron photomicrographs of abactinal spinelets from plates of dorso-lateral area at base of ray of *Nepanthia* species. **a.** *Nepanthia belcheri*, WAM 613-77, Townsville, Qld.; **b.** *N. belcheri*, WAM 935-76, Dampier, W.A.; **c.** *N. briareus*, WAM 56-79, Moluccas, Indonesia; **d, e.** *N. crassa*, WAM; **f.** *N. gracilis* sp. nov., holotype, WAM 103-78, Philippines; **g.** *N. fisheri* sp. nov. holotype, WAM 102-78, Sabah; **h.** *N. maculata*, WAM 587-75, Dampier, W.A.; **i.** *N. maculata*, WAM 57-79, Moluccas, Indonesia; **j, k,** *N. nigrobrunnea* sp. nov., holotype, AM-J 10147 N.S.W.; **l.** *N. troughtoni*, WAM 570-75, Esperance, W.A.

7. INTER-RELATIONSHIPS OF RECENT STALKED, NON-ISOCRINID CRINOIDEA

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SUMMARY

Outlines are given of the body form in the extant families of the stalked crinoid orders Millericrinida and Bourgueticrinida with particular notes on the few taxa exhibiting secondary arm branching.

The recent nominal species of the Bourgueticrinida are listed in a table, together with their distributions and an indication of the size range of the often limited known material. The wisdom of division of these taxa into more than the one family Bathycrinidae is questioned, in view of recent observations on ontogeny and variation, particularly with regard to the stalk attachment.

A new record of a particularly relevant species, *Porphyrocrinus thalassae* Roux, is included, with a photograph showing the secondary arm branching.

INTRODUCTION

Apart from the aberrant Holopodidae (order Cyrtocrinida), the remaining recent non-Isocrinid taxa of stalked Crinoidea are referable to two orders — the family Hyocrinidae to the Millericrinida and the remainder to the Bourgueticrinida. Most of these species are remarkable among recent crinoids for the conspicuous part the basal plates play in making up the calyx of the adult.

SYSTEMATIC ACCOUNT

The Hyocrinidae have thin-walled cup-shaped calyces, surmounted by the arms, which are more or less widely-spaced, approximately cylindrical in cross-section and unbranched in most genera, including *Hyocrinus*. However, *Calamocrinus diomedae* from near the Galapagos Islands, representative of a monotypic genus, has irregularly-branching arms, evidently formed by elaboration of up to five of the original pinnules on each side of a primary arm into secondary arms, themselves bearing pinnules. This kind of augmentation of arm number contrasts with the multiplication by what is called 'adolescent autotomy' at proximal syzygies followed by regeneration, with the first new ossicle becoming an axillary, found throughout the Comatulida. The single exception in this order is *Comatula rotalaria* Lamarck, from northern Australia, in which the second brachial of each of the ten primary arms of the post-pentacrinoid gradually transforms itself into a symmetrical axillary by modification of its appendage into an arm instead of a pinnule. Similar arm multiplication also occurs in some Isocrinida.

The species of the Bourgueticrinida differ from the Hyocrinidae in having the calyx more compact and thick-walled, bearing closely approximating arms lacking pinnules on usually the first six to ten brachials. The nominal species currently recognised are listed in Table 1. However, some of these names are very likely to prove to be synonymous since many are abyssal and many are only known from incomplete specimens often of a limited size range, so that inadequate allowance has often been made for very wide geographical distributions and for growth changes when naming supposedly new taxa.

The first five genera in Table 1 have been referred to the family Bathycrinidae, three of them: *Rhizocrinus*, *Conocrinus* and *Democrinus*, having five simple arms while *Bathycrinus* and

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*Monachocrinus** have ten arms, the second post-radial ossicle being a primary axillary. All have the arm bases aligned vertically when in the non-feeding position with a marked lateral flange on each side, beyond which basal part the muscular and non-muscular joints between the brachials normally alternate regularly. The calyx ranges in form from conical to narrow vase-shaped and the stalk is xenomorphic with some of the topmost columnals discoidal, their joint faces more or less smooth and not yet modified into the oval synarthries found between the succeeding more elongated columnals, the alignment between the synarthrial joints being twisted from one to the next through nearly 90°. The distal part of the stalk, when known, bears irregular rhizoid-like jointed appendages for attachment, though in a few cases, notably *Democrinus brevis* A. H. Clark (see A. M. Clark, 1977) the rhizoid system is more or less completely replaced by an irregular flattened expansion at the end of the stalk.

In 1907, A. H. Clark proposed a new family Phrynocrinidae for *Phrynocrinus nudus* from SE of Japan, a species with all the columnals fairly short and twisted so that successive joints appear alternately wide and narrow when seen in one plane, distal attachment is solely by an expanded terminal plate, the calyx is markedly flared above bearing almost cylindrical arms which leave exposed the relatively large disc or tegmen and which often have several successive muscular joints easily outnumbering the non-muscular joints by about 4:1. Judging from what is left of the three least broken post-radial series of the holotype, the five primary arms branch irregularly at least once, these three having axillaries at brachials 13, 20 and 25 respectively, all preceded by pinnules. It is likely that this development of secondary arms is by modification from pinnules, as in *Calamocrinus*.

Subsequent discoveries of recent Bourgueticrinida have tended to blur the distinction between Phrynocrinidae and Bathycrinidae.

In 1973, I described an Atlantic species, *Zeuctocrinus gisleni*, referring this new genus to the Phrynocrinidae, on account of its low, flared calyx, rounded arm bases and the similar form of the stalk to that of *Phrynocrinus nudus* with synarthrial joints throughout (at least in larger specimens), though unfortunately the stalk attachment is unknown. However, smaller specimens of *Zeuctocrinus* than the holotype of *Z. gisleni*, show that earlier in the ontogeny the upper columnals are much shorter and the distal ones relatively longer. Possibly the same will prove to be true of *P. nudus*, when a better range of specimens is available. *Z. gisleni* parallels *Bathycrinus* in having a primary axillary — normally the second post-radial ossicle — and ten arms and also shows the same relatively high frequency of non-muscular joints in the arms as *Bathycrinus*, only a few proximal brachials having muscular joints at both ends.

In 1912, A. H. Clark described *Naumachocrinus hawaiiensis*, a species with stalk attachment

*In 1970 I noted that A. H. Clark's figure of the holotype of *Monachocrinus sexradiatus* (1923) appeared to show muscular joints at both ends of brachials 3, 6 and 9, as characteristic of *Bathycrinus*, where *Monachocrinus* is diagnosed by Gislén (1938) as having complete alternation of muscular and ligamentary joints. However, thanks to Dr. Madsen, I have been able to see the holotype and find that only one arm out of those remaining has muscular joints at both ends of brachial 3 and its condition beyond brachial 5 is unknown due to breakage. Nevertheless, the joint sequence hardly seems of generic weight unsupported. Other distinctions cited by Gislén are the fusion of the basal ring in *Bathycrinus*, while some specimens at least of *Monachocrinus* (e.g. the paratype of *M. sexradiatus* but not the holotype) show distinct interbasal sutures, and the profile of the calyx showing an angle between the basal and radial rings in *Bathycrinus* but a straight line or smooth curve in *Monachocrinus*. The importance of the latter was stressed by Macurda & Meyer (1976). It seems to me likely that fusion of the basal ring may be correlated with a higher incidence of autotomy between the two rings and so be more frequent in *Bathycrinus*. The subsequent regeneration of the radial ring and arms would result in at least temporary discontinuity of the profile. Conversely, some specimens of *Bathycrinus* do show smooth profiles, along the radii if not also the interradii, either by slight constriction of one or the other ring near the junction point or by an even flaring of both rings. The second is true of the specimen of *B. australis* shown in Döderlein's pl. 5, fig. 1 and pl. 6, fig. 7 (1912), which incidentally also shows distinct interbasal sutures as photographed in toluol in pl. 6. I consider therefore that the generic distinction of *Monachocrinus* from *Bathycrinus* is ill-founded.

similar to that of *Phrynocrinus*, prompting him to refer the genus to the Phrynocrinidae although he said that the upper part of the stalk resembled that of *Rhizocrinus* (now *Democrinus*) *weberi* and the calyx is almost perfectly cylindrical with extraordinarily long radials but a basal ring no higher than the discoidal uppermost columnal just below it (see A. M. Clark, 1973, Fig. 6h). The arms are unknown.

A fourth genus — *Porphyrocrinus* — has also been referred to the family Phrynocrinidae, after considerable deliberation by Gislén (1925), because the type-species, *P. verrucosus* from Indonesia, has simple arms, proximally flanged and concealing the tegmen, the calyx is almost cylindrical and the proximal columnals are discoidal. The stalk attachment is unknown. Consequently there is very little superficial resemblance to *Phrynocrinus*, though more to *Naumachocrinus*. However, in 1973 I described a similar species from the SW Indian Ocean, *Porphyrocrinus polyarthra*, from a specimen retaining the distal part of the stalk, showing that attachment is by a lobed terminal expanded plate. Even so, the anomalies between *Porphyrocrinus* and *Naumachocrinus*, on the one hand, and *Phrynocrinus* on the other, seemed to me so great that I proposed a third family, Porphyrocrinidae, intermediate between the two others, characterized by the stalk attachment of the Phrynocrinidae and the calyx form of the Bathycrinidae.

Subsequently, two factors affecting the validity of this third family and perhaps even of the Phrynocrinidae, have become evident.

Recently both Roux and I have independently found a new bourgueticrinid which he described as *Porphyrocrinus thalassae* in 1977. Smaller specimens of this species (upper stalk diameter c.3 mm) have simple arms but the larger ones (s.d. c.4 mm) have the first pinnule, on the right side of the eighth brachial (Br_8) modified into a secondary arm and may also have the first pinnule of the left side (on Br_{10}) similarly modified, converting these two ossicles into rather lop-sided axillaries. Possibly at a larger size still the secondary arms achieve equality with the primary ones and adopt a plane tangential to the vertical axis instead of being inclined obliquely like the pinnules; the axillaries would then become more nearly symmetrical. Since the holotypes of the other species of *Porphyrocrinus* were smaller, it is not unlikely that they too may show a similar augmentation in arm number with growth.

Secondly, re-examination of the type material of *Democrinus brevis*, brought home to me in 1977 the great variation in stalk attachment shown by different species of undoubted Bathycrinidae, *D. brevis* showing expanded terminal plates in contrast to both *D. parfaiti*, the type-species of *Democrinus*, and some West Indian specimens which I have attributed to *D. conifer*, which consistently have slender branching rhizoids terminating the stalk. Macurda (in Meyer, Messing and Macurda, 1978) believes that *D. brevis* and *conifer* intergrade. Also McKnight (1977) has described a bathycrinid stalk from the Kermadec Islands which terminates in both an expanded plate and rhizoids. Gislén's 1927 diagnosis of the Bathycrinidae as having stalks attached by rhizoids needs modification. As indicated in Table 1, in about a third of the nominal species of Bathycrinidae the distal part of the stalk is unknown.

Hopefully, the current increase in the amount of deep-water biological collecting and the number of specialists interested in these animals may soon result in some degree of clarification of the inter-relationships of these recent Bourgueticrinida.

NOTE ON AN UNRECORDED SPECIMEN OF *PORPHYROCRINUS THALASSAE* ROUX

Porphyrocrinus thalassae Roux
Fig. 1

Porphyrocrinus thalassae Roux, 1977: 34-38, 50-54, fig. 1B, pl. 1, figs. 1-5.

MATERIAL EXAMINED: 'Discovery' station 8511/2, 41°49′N, 11°06′W (NW of Spain), 2574-2584 metres; 1 specimen.

REMARKS: Only the uppermost 30 columnals remain, measuring 15 mm. The first 20 are discoidal, the height of the uppermost one being 0.3 mm, while the thirtieth is 1.5 mm high. Stalk diameter at the top is 4.1 mm and at the bottom 3.2 mm.

The basal ring height is 1.0 mm radially, 2.0 mm interradially. The radial ring is 1.4 mm high radially. The total calyx height is 2.4 mm radially and 2.8 mm interradially. The top of the basal ring is slightly constricted after a slight expansion so that both top and bottom are 4.1 mm in diameter. The top of the radial ring is 5.2 mm in diameter. The interbasal sutures are not distinguishable, the undulating basiradial suture only after removal of the skin but the interradial sutures are more easily visible.

The first eight post-radial ossicles are joined in pairs by non-muscular joints, 1+2, 3+4, 5+6, 7+8ax., Br_8 bearing a secondary arm on the right. Two rays, C and E, have another secondary arm on the left of Br_{10}. Four of the arms from Br_8 have the first brachial divided longitudinally; non-muscular joints mostly alternate with muscular ones from 2+3 onwards so that the first pinnule is on the outer side of Br_3. The primary arms have their first pinnule on the right of Br_{12}. This consists of 13 very elongated pinnulars with a short gonad from segments 2-5; the length is 11.5 mm. The longest arm remaining is a secondary one; it measures 60 mm and consists of 50 brachials; probably c.20 mm is lost. Some of the more distal brachials have a muscular joint at both ends. The dark brown tegmen is widely exposed between the bases of the primary arms; it extends to about Br_6.

The numerology of the ossicles is debatable but, as the additional arms are clearly secondary, the first eight post-radial ones are not a true division series and are better counted as brachials. The numerology used by A. H. Clark in 1907 in describing **Phrynocrinus nudus** was that of Carpenter, counting the ossicles on both sides of the ligamentary joints as forming a single brachial. Translating to Clark's later method of counting, as now generally adopted, the joints of the holotype of *P. nudus* are as follows:
1+2, 3, 4+5, 6, 7+8, 9, 10, 11, 12+13, 14, 15+16, 17, 18, 19+20, 21, 22, 23, 24+25ax.
1+2, 3, 4+5, 6, 7, 8, 9, 10, 11, 12, 13+14, 15, 16, 17+
1+2, 3, 4, 5+6, 7, 8+9, 10, 11, 12+13, 14, 15+16, 17, 18, 19+20ax.
1+2, 3, 4+5, 6, 7+8, 9, 10+11, 12, 13, 14+15, 16, 17, 18+
1+2, 3, 4+5, 6, 7, 8, 9+10, 11, 12, 13ax.

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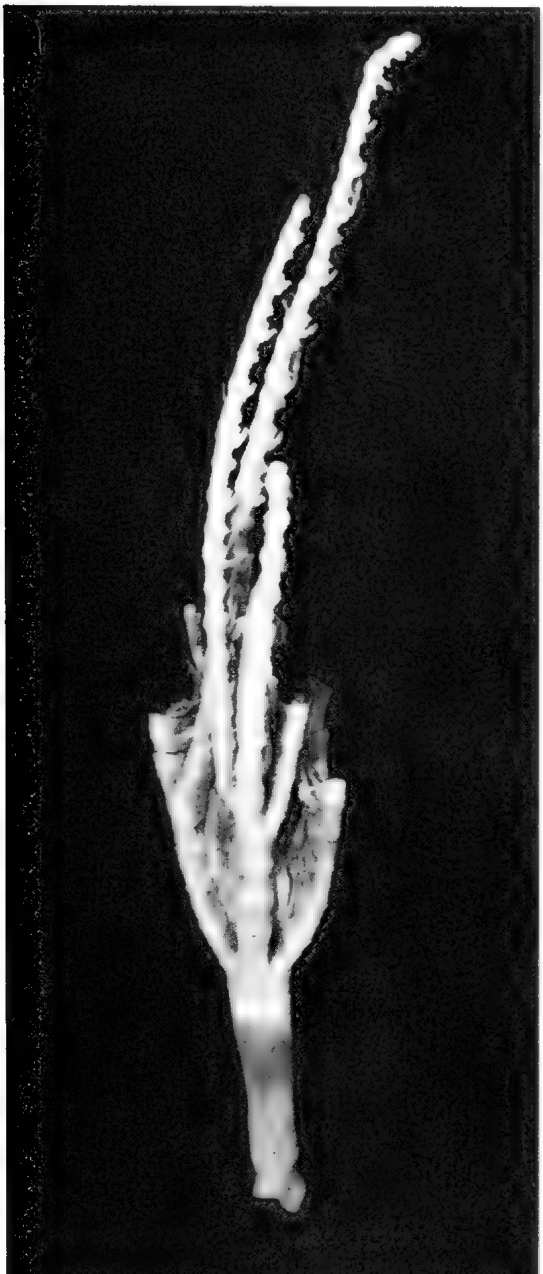

Fig. 1. *Porphyrocrinus thalassae* Roux, 'Discovery' st. 8511/2, showing the secondary arm branching. The calyx has been partially bleached to clarify the sutures.

Table 1. Species of recent Bourgueticrinida, showing the occurrence of the distal part of the stalk and of at least part of the arms beyond the first brachial, entries in brackets indicating broken and incomplete or regenerating parts in the recorded material. The first column gives an approximate estimate of the size range, this measurement has not always been cited and entries with '?' '??' signify the degree of guesswork involved.

	Proximal stalk diameter: approx. range (mm)	Distal Stalk	Arms beyond Br_1	Depth Range	Geographical range
Bathycrinus aldrichianus W.T.	0.5-0.75	+	+	3320-5850	Mid-Atlantic
australis (A.H.C.)	1.0-2.0	+	+	1730-8210	Southern Ocean
australocrucis McK.	1.0	+	+	693-838	New Zealand
carpenteri (D. & K.)	0.75-1.25	+	+	1360-2810	Arctic N. Atlantic
complanatus A.H.C.	? 1.25-2.0?	+	+	2840	Bering Sea
equatorialis A.H.C.	? 1.0 ?	?	–	4220	Mid-Pacific
gracilis W.T.	0.25-0.75	–	+	4450-5010	NE Atlantic
pacificus A.H.C.	? 1.0 ?	(+)	+	1650	S Japan
woodmasoni A.H.C.	—	–	–	2770	Bay of Bengal
Monachocrinus aotearoa McK.	1.25	+	+	1060-2150	New Zealand
caribbeus (A.H.C.)	? 0.5 ?	–	–	1260	West Indies
mortenseni Gislén	0.25	–	+	1000	New Caledonia
paradoxus (A.H.C.)	? 0.5 ?	(+)	+	2370	Bay of Bengal
perrieri (K. & V.)	0.25	–	(+)	1620-4600	Azores, S. Africa
recuperatus (Perr.)	1.25-1.75	–	+	2300-4260	Azores, Morocco
sexradiatus A.H.C.	0.5	+	+	2075	Iceland
Rhizocrinus lofotensis Sars	0.5-1.0	+	+	140-3475	N Atlantic
minimus (Död.)	0.25	–	(+)	1300	East Indies
Conocrinus cabiochi Roux	1.0	-	–	1975-2070	Bay of Biscay
cherbonnieri Roux	0.5	-	–	330-510	Bay of Biscay
Democrinus aoteanus McK.	1.0	+	+	650-945	New Zealand
brevis (A.H.C.)	1.5-1.75	+	+	540	West Indies
chuni (Död.)	0.25-1.25	+	+	410-1800	E & S Africa
conifer (A.H.C.)	1.75	–	–	160-1750	Brazil
globularis Gislén	1.25	–	–	290	East Indies
japonicus Gislén	1.25	+	+	140-170	S Japan

nodipes (Död.)	0.25	+	+	1160-1570	East Indies
parfaiti Perr.	1.0-1.5	+	+	600-4260	NE Atlantic
poculum (Död.)	0.25	(+)		1570	East Indies
rawsoni (Pourt.)	1.5	(+)	+	70-650	West Indies
weberi (Död.)	0.5-4.25	+	+	110-2050	
Phrynocrinus nudus A.H.C.	4.0-6.0	+	+	600-1190	SE Japan
Naumachocrinus hawaiiensis A.H.C.	1.5	+	–	930-1300	Hawaiian Is.
Zeuctocrinus gisleni A.M.C.	0.75-2.75	-	+	2110-2575	NE Atlantic
Porphyrocrinus incrassatus Gislén	0.75	+	(+)	1300-2400	E Atlantic
polyarthra A.M.C.	1.0-1.25	+	(+)	400	SW Indian Ocean
thalassae Roux	2.0-4.0		+	2110-2580	Bay of Biscay
verrucosus Gislén	1.5	–	+	345	East Indies

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8. DEEP-SEA ECHINODERMS IN THE TONGUE OF THE OCEAN, BAHAMA ISLANDS: A SURVEY, USING THE RESEARCH SUBMERSIBLE *ALVIN*.

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SUMMARY

Deep-sea echinoderms of the Tongue of the Ocean, Bahama Islands, have been studied, using trawled collections made by the University of Miami together with observations from the deep submersible *Alvin*. Transect runs in the submersible permitted studies of population densities and behaviour of approximately 38 species of larger invertebrates, of which 27 were echinoderms. Several echinoderm species show a patchy distribution pattern which is apparently not related to available food resources. Some species are exclusively herbivores, feeding on fragments of turtle grass, *Thalassia testudinata* and sargassum weed, *Sargassum* spp. Feeding habits of some Tongue of the Ocean echinoderms are compared with those of the same species from further north, where supplies of plant material are not nearly so abundant.

Trawled collections of echinoderms do not include some of the most common and ecologically important holothurians; conversely, some burrowing species very common in the area were not observed from the *Alvin*. Further observations were made on swimming behaviour of holothurians. All swimming forms studied apparently derive nourishment from the seafloor. Short tracks on the seafloor indicate that swimming behaviour is a common means of transportation from one area to another. The ophiuroid *Bathypectinura heros* is capable of active swimming movements. Uniformly conical mounds on the seafloor are often built up around a central core of holothurian faeces.

INTRODUCTION

During January, 1977, a series of eight dives were made in the submersible D.S.R.V. *Alvin*, to depths in excess of 3,660 metres, in the Tongue of the Ocean, Bahama Islands. The purpose of the dives was to make ". . . first-hand observations . . on the biology of deepwater benthic fishes and larger invertebrates and to take qualitative and quantitative data by visual and photographic methods" (D. M. Cohen, 1 March 1977, Cruise Report NOAA — MUST dives with D.S.R.V. *Alvin* in the Bahamas — unpublished).

I was able to participate in four dives, and on one, Dive 703, an excellent opportunity was provided to make quantitative studies of echinoderms and other large invertebrates, and to observe activities of echinoderms. This paper represents for the most part the results obtained during Dive 703, although some aspects of "natural history" of echinoderms were obtained during one or more of the other dives in which I participated. Additional information on echinoderms from the Tongue of the Ocean was obtained from the extensive collections of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, whose staff members have occupied numerous trawl stations in the Tongue of the Ocean over the past several years.

METHODS

1. LOCATION OF ALVIN DIVE 703 AND DESCRIPTION OF ACTIVITIES

Dive 703 was made on January 12, 1977 in the Tongue of the Ocean, Bahama Islands

24°54.9'N, 77°41.1'W, at a depth of 1938-2141 metres. Total time on bottom 5.6 hours. Pilot, Dudley Foster, observers Daniel M. Cohen and David L. Pawson.

During Dive 703 a total of 11 measured transects were run. Transect 9 was aborted because of a malfunction in the metre wheel which was used to measure the distance traversed by the submersible. Transect runs were essentially consecutive, and were made in a south to south-easterly direction (see Table 1). Thus, no overlap of transect runs occurred.

Table 1. Transect runs covered by *Alvin*, Dive 703. Transect 9 was aborted due to equipment malfunction.

Transect	compass heading	distance run (m.)	area studied (m^2)
1	180	914	3,654
2	180	679	2,716
3	154	202	808
4	164	716	2,864
5	145	419	1,676
6	143	445	1,880
7	148	138	552
8	121	267	1,068
10	138	188	752
11	138	289	1,156
		4,257 metres	17,126 sq. metres

It has been estimated that an observer can see out for a distance of approximately 4 metres from the observer's viewing port in the pool of light thrown by the submersible's floodlamps. Knowing this distance, and knowing the distance traversed by the submersible during a transect run, it is possible to calculate the total area studied during a run, and then to determine the number of specimens of a particular species occurring per unit area. In the table shown here, population densities are expressed numbers of individuals per 1,000 m^2 (Table 2).

In order to estimate the accuracy of population counts made through the viewing port, a comparison was made between numbers of animals photographed in early transects by an E.G. & G. camera mounted on the submersible and numbers of animals counted, and results obtained were closely similar. A complete photographic survey for all transects was not possible because of the limited amount of film in the single camera.

The bottom was composed of a firm to flocculent greyish to light brown sediment, which contains very numerous pteropod mollusk shells of several species. Fragments of the floating alga, *Sargassum* spp., and roots and blades of turtle grass, *Thalassia testudinata* are ubiquitous on the seafloor (figs 1a, 1b). In a few areas they form mats, but for the most part the fragments seem to be more or less evenly scattered.

2. IDENTIFICATION OF ECHINODERMS VIEWED FROM ALVIN

Through the courtesy of Dr Gilbert L. Voss, I was able to examine the invertebrates collected by the Rosenstiel School of Marine and Atmospheric Science in the Tongue of the Ocean. This enabled a positive identification to be made of most of the echinoderms seen from the Alvin. Some systematic problems yet remain to be resolved.

Furthermore, the opportunity was taken to investigate stomach contents of selected species of ophiuroids and echinoids, so that feeding propensities could be determined. The University of Miami collections also included specimens of echinoderm species which are apparently common in the study area but were not observed during Alvin Dive 703. These taxa are

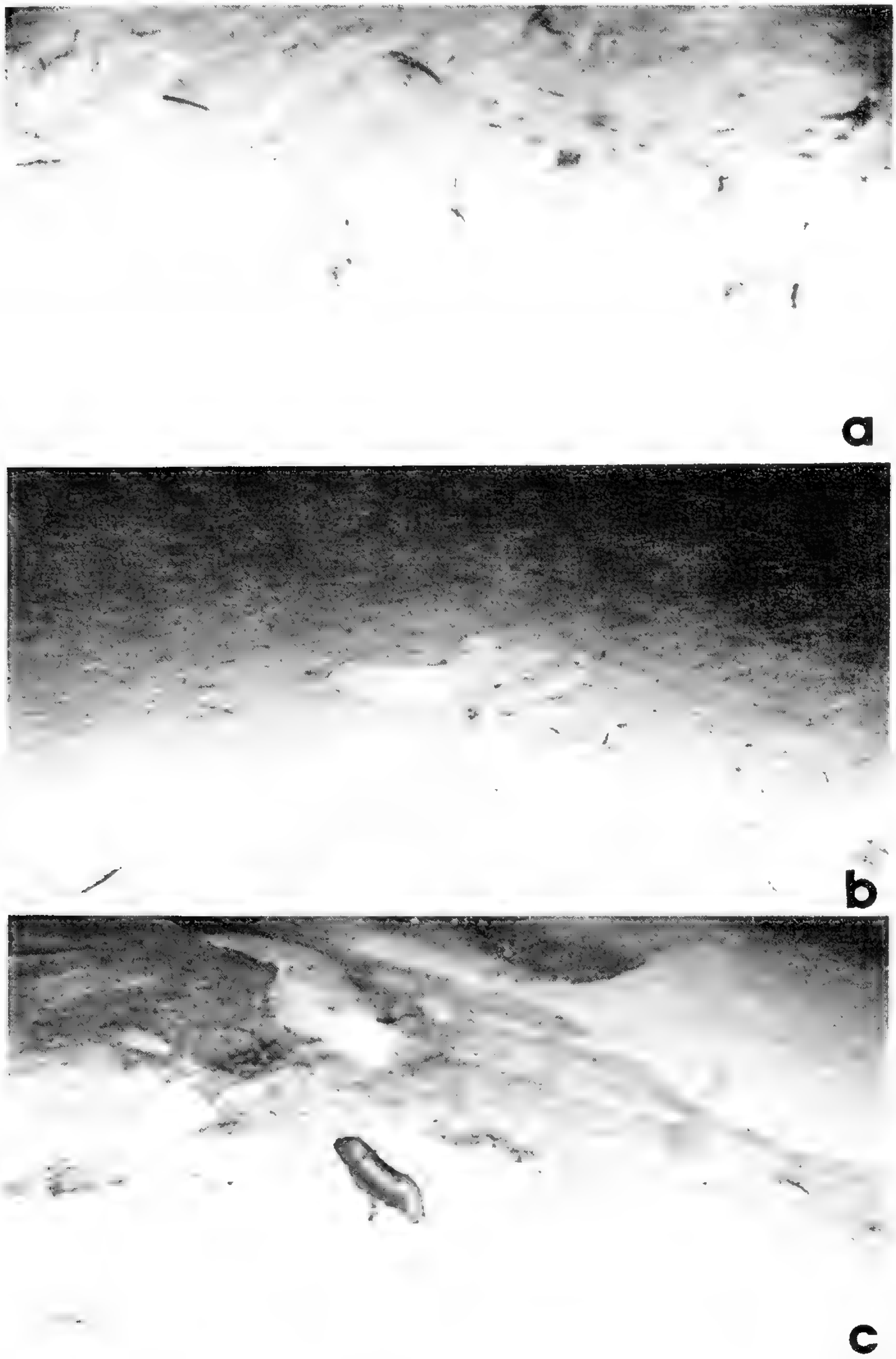

Fig. 1. Seafloor features. 1a, scattered fragments of *Thalassia* and *Sargassum* spp. Photo: D. M. Cohen. 1b, short track left by swimming holothurian, *Benthodytes*. 1c, *Benthodytes lingua* near rock outcrop.

discussed below.

RESULTS AND DISCUSSION

1. SPECIES STUDIED

During the ten successful transect runs, counts were made of 38 species of larger invertebrates. These comprise one sponge (*Euplectella suberea* Thomson, included in Table 2 for purposes of comparison of population densities), four coelenterates ("pennatulacean", *Cerianthus* sp., *Anthomastus* sp. and *Umbellula* sp.), three crustaceans (*Glyphocrangon* sp., penaeid shrimp — *Hepomadus* sp.?, hermit crab), one pycnogonid (*Colossendeis colossea* Wilson), and two mollusks (white gastropod and octopus). The remaining 27 species were echinoderms, as follows—

ECHINOIDEA: *Hygrosoma petersi* (Agassiz), *Phormosoma placenta* Thomson, *Plesiodiadema antillarum* (Agassiz), *Salenocidaris profundi* (Duncan), *Brissopsis elongata* Mortensen; dead tests.

HOLOTHUROIDEA: *Ellipinion delagei* (Herouard), *Benthodytes typica* Théel, *Benthodytes sanguinolenta* Théel, *Benthodytes lingua* Perrier, *Psychropotes depressa* (Théel), *Enypniastes eximia* Théel, *Deima validum* Théel, *Pseudostichopus* species A, *Pseudostichopus* species B, *Mesothuria verrilli* (Théel), *Paelopatides* sp.

ASTEROIDEA: *Nymphaster arenatus* (Perrier), *Ceramaster grenadensis* (Perrier), *Zoroaster fulgens* (Thomson), *Freyella* species A, *Freyella* species B, "*Luidia*".

OPHIUROIDEA: Bathypectinura heros (Lyman), *Ophiomusium* species A, *Ophiomusium* species B, "red ophiuroid".

CRINOIDEA: "ten-armed sea lily".

A few other species of echinoderms were seen but not counted. These included numerous specimens of small pink ophiuroids (Family Ophiacanthidae?) clinging to sponges and small rocks, and pinkish five-armed euryalid ophiuroids, also clinging to sponges.

2. COMMON TONGUE OF THE OCEAN ECHINODERMS NOT COLLECTED BY THE UNIVERSITY OF MIAMI

The following species of holothurians are common in the area studied, but are not represented in the University of Miami collections: *Ellipinion delagei* (Herouard); *Enypniastes eximia* Théel; *Paelopatides* sp.

The first and last species were found to be numerically dominant in some transects (see Table 2). These species were not collected in trawls because they are exceedingly fragile and would be reduced to gelatinous masses in trawl samples. Furthermore, they are barely negatively buoyant, and are easily dislodged by the bow wave of the submersible; the bow wave of a trawl would have the same effect, materially reducing the possibilities of capturing specimens of these species. These species are highly important elements in the benthic biota of the area and their influence upon the composition and structure of sediments is undoubtedly important.

3. COMMON TONGUE OF THE OCEAN ECHINODERMS COLLECTED BY THE UNIVERSITY OF MIAMI, BUT NOT OBSERVED FROM THE ALVIN.

The following species of holothurians are common in the area studied, but were not observed during *Alvin* transects: *Molpadia barbouri* Deichmann; *Molpadia musculus* Risso;

Table 2. Population densities of echinoderms (and the sponge, *Euplectella*) observed during *Alvin* Dive 703. Densities are expressed as number of specimens per 1,000 m^2.

	Transect number — *Alvin* Dive 703									
Ophiuroidea	1	2	3	4	5	6	7	8	10	11
1. *Bathypectinura heros*	26.2	67.6	98.8	33.9	1.2	0	3.6	14	0	0
2/3. *Ophiomusium* sp. A/B	2.1	100 +	0	0	1.2	0.5	0.2	1	1.4	0
4. Red ophiuroid	0.6	0	0	0	0	0	0	0	0	1.7
Asteroidea										
1. *Nymphaster arenatus*	0.54	0.74	0	0.35	1.2	2.2	4	1	0	0
2. *Zoroaster fulgens*	0.8	0	0	0	1.8	3.9	0	0	0	0
3. *Ceramaster grenadensis*	1.6	0.4	0	0	1.8	0	0	0	0	0
4. *Freyella* sp. A (6 arms)	0.3	0	0	0	0.6	1.7	0	0	0	0
5. *Freyella* sp. B (11 arms)	0	0	0	0.6	0	0	0	0	0	0
6. "*Luidia*"	0	0	0	0.3	0	0	0	0	0	0
Echinoidea										
1. *Hygrosoma petersi*	22.7	33.8	35.8	21	14.9	17.4	52.7	8.4	16	19
2. *Plesiodiadema antillarum*	30.5	44.9	51.9	0.8	0	0	0	0	0	0
3. *Phormosoma placenta*	12.7	15.1	3.7	3.5	7.7	4.5	18.2	2.8	6.7	7.8
4. *Salenocidaris profundi*	1.62	8.5	1.2	1.0	0	0	0	0	0	0
5. *Brissopsis elongata* (dead)	0	0	0	0	2.4	0.6	20	0.4	0	0
Holothuroidea										
1. *Ellipinion delagei*	29.5	45.2	0	2.1	45.2	175.3	852.7	79.4	0	0
2 3. *Benthodytes typica sanguino*	60	74.3	85	122.3	300 +	9	9.1	7.5	0	0
4. *Psychropotes depressa*	7.6	12.5	13.6	22.4	39.3	41	298	186.9	84	140.5
5. *Benthodytes lingua*	2.7	5.1	1.2	11.9	16.1	39	227.3	38.3	6.7	37.9
6. *Enypniastes eximia*	0.5	0	0	1	0	0	2	0	0	0
7. *Deima validum*	0.3	0	0	0	0	0	0	0	0	0
8. *Mesothuria verrilli* 9/10. *Pseudostichopus* A/B	6.5	8.8	3.7	5.9	7.1	4.5	3.6	2.8	0	0.9
11. *Paelopatides* sp.	4	8.5	0	5.9	74.4	167	169.1	68.2	8	44
Crinoidea										
1. Ten-armed sea lily	0	0	0	0.7	1	0.6	0	0	1.4	0
Porifera (sponges)										
1. *Euplectella suberea*	9.5	14.3	13.5	20.6	19	9.6	87	5.6	0	1.8

Gephyrothuria glauca (Clark).

The three holothurian species are apparently all burrowing forms. *Molpadia* species are known to be active burrowers (Clark, 1907; Rhoads and Young, 1971). It is surprising that *Gephyrothuria glauca*, with its dorsal whip-like papillae, is also apparently an infaunal species. It might have been expected that this species uses its papillae as sensory devices in a manner similar to that of the elasipodids, and that the animal is an epifaunal dweller.

Dead tests of the spatangoid echinoid *Brissopsis elongata* were observed during some transects (see Table 2); live specimens of this species were undoubtedly burrowed into the substratum in the same areas, but no trace of their burrows was visible from the *Alvin*.

It is evident from the above discussions that ecological studies of larger deep-sea invertebrates based entirely upon observations from submersibles or upon trawled samples might not necessarily reflect the true situation on the seafloor, and some of the most important "consumers" will be unwittingly omitted from consideration. It is important to remember that some of the most effective reworkers of sediments might not be represented in trawls or in photographs taken by submersibles.

4. INTESTINE CONTENTS OF SELECTED SPECIES

The intestine contents of several species of echinoderms collected in the Tongue of the Ocean by the University of Miami were examined, in order to determine which species might be using as food the fragments of seaweed and turtle grass that are scattered over the seafloor in that area. Vegetarian feeding habits are commonplace among the echinoids (Lawrence, 1975) but other echinoderms seem to be less inclined towards such a diet. In the case of two species of echinoids, comparisons were made with specimens collected from further north, where plant material is not nearly so abundant, but is nonetheless present, as Menzies et al. (1967) and Menzies and Rowe (1969) have shown for *Thalassia* and as Schoener and Rowe (1970) have shown for *Sargassum* spp.

a. *Hygrosoma petersi:* In all Tongue of the Ocean specimens examined, intestine contents consisted almost exclusively of fragments of *Sargassum* and fragments of *Thalassia*. Presence of occasional pteropod shells and foraminiferal skeletons indicate that some sediment is also ingested, but this may be accidental. Usually *Sargassum* dominated in intestines examined. Many *Sargassum* fragments carried colonies of encrusting bryozoans; apart from these, and the skeletal remains mentioned above, no other animal materials were found in the intestines. Specimens collected from further north (see Table 3), between Georgia and New York, appeared to have a more "mixed" diet, indicating that when abundant plant material is not available locally, this species can subsist on organic material extracted from sediments.

Mortensen (1935) studied specimens of this species from South Africa, West Indies and southwest Ireland, and found that the intestines contained ". . . only mud, formed into small balls about the size of peas." (p. 205). In a later paper, Mortensen (1938) noted that the Pacific species *Hygrosoma luculentum* (Agassiz) had its intestines filled with "bits of plants" (p. 226).

b. *Phormosoma placenta:* Intestine contents of this species in the Tongue of the Ocean consisted exclusively of small mud balls 1-3 mm in diameter, bound together by mucus. Several specimens from elsewhere in the Eastern Atlantic had similar mud balls in their intestines. This observation concurs with that of Mortensen (1935).

c. *Plesiodiadema antillarum:* Intestine contents poorly defined mud balls, not strongly bound by mucus. No plant material. Mortensen (1938, 1940) notes that *P. indicum* from the Indo-Pacific eats pieces of plants almost exclusively. Despite the abundance of plant material in the area, *P. antillarum* does not appear to ingest it.

Table 3. Size and intestine contents of *Hygrosoma petersi* from between Georgia and New York.

Albatross Station	Diameter of test (mm)	Intestine contents
2678 32°40′N, 76° 40′30′′W; 1,315 m	95	mostly mudballs, 3 mm in diameter, also a few *Sargassum* fragments
	110	indeterminate plant and animal fragments
	135, 145	*Sargassum* fragments and mud
	150	*Sargassum* fragments, some with encrusting bryozoans
2115 35°49′30′′ N, 74° 34′45′′ W; 1,517 m	155	unidentifiable weed fragments
2721 38°56′ N, 72° 11′30′′ W; 1,463 m	155	mostly mudballs 3 mm in diameter; few unidentifiable weed fragments
2181 39° 29′N, 71° 46′W; 1,258 m	150	Mudballs of various sizes, unidentifiable weed fragments
2691 39° 37′N, 71°08′ W; 1,503 m	155	mostly *Sargassum* fragments with very few mudballs 3-4 mm in diameter.

d. *Salenocidaris profundi:* Intestine contents poorly defined mud balls; no plant material.

e. *Ophiomusium* spp.: The two species of *Ophiomusium* apparently consume nothing but sediment, perhaps on a non-selective basis. In most specimens examined the stomachs were virtually empty; in a few, the stomach was filled with sediment.

f. *Bathypectinura heros:* Of approximately 20 specimens examined, all but two had empty stomachs. The two exceptions contained exclusively fragments of *Sargassum*. Some of the "empty" stomachs contained a dark brown finely divided material that may once have been pieces of *Sargassum*. Madsen (1973) examined "a few stomach contents" (p. 142) of this species and found them to include mainly unidentifiable organic detritus, foraminiferans, etc. This then is the first record of a vegetarian diet in this species. Fell (1952) made the remarkable observation that the related shallow water New Zealand species *Pectinura maculata* (Verrill) can feed on anthers of the southern beech tree, *Nothofagus* sp., which fall into the water from overhanging trees. Schoener and Rowe (1970) found that another deep-sea ophiuroid, *Amphiophiura bullata* (Lyman), is capable of ingesting and presumably using as food bladders of *Sargassum*.

5. SOME ASPECTS OF BEHAVIOUR AND MORPHOLOGY OF SELECTED SPECIES

Hygrosoma petersi. This large, conspicuous and fast-moving epibenthic echinoid is common in several areas of the Atlantic Ocean in depths of 200-2,870 m (Mortensen, 1935). Grassle et al. (1975) note that the species is very active, and include an excellent photograph of a specimen in situ. Tongue of the Ocean representatives of this species differ in some respects from their conspecifics further to the north, which were observed by the author during *Alvin* Dive 592, at a depth of 1930-1988 m, in the area of Deepwater Dumpsite 106, 39°09.9'N, 71°54.8'W. The Tongue of the Ocean form has much smaller and less conspicuous hooves on the oral spines (see figs 2a, 2b), although in all other respects this form conforms to the traditional concept of the species.

These specimens also showed behavioural differences from the specimens observed during *Alvin* Dive 592. When being approached by the submersible, the northern specimens, upon sensing the bow wave (or the lights) would immediately "gallop" away from the source of the disturbance. The Tongue of the Ocean specimens were less inclined to move away rapidly; in many cases they remained in position, but directed their aboral spines away from the source of the disturbance.

Ellipinion delagei reached great population densities in some areas, especially during transect 7. This species is almost completely transparent when alive, and the body is virtually colourless. Through the body wall the coiled sediment- filled intestine can be clearly seen. Barham et al. (1967) and Pawson (1976) have found that some elasipodids tend to be oriented so that their anterior ends face into the prevailing current. In the case of *Ellipinion*, this tendency was exhibited to some extent, but was not rigidly followed. In some areas all specimens appeared to be facing in the same direction (fig. 2c), while in others a more random pattern of orientation was observed. In the study area there was almost no detectable current activity, and it is possible that in the absence of a significant current, the animals have a rather random orientation.

Benthodytes typica in the Tongue of the Ocean is generally light brownish to cream, with little evidence of shades of red. The anterior end is dark brown. This species was not observed to swim, not even when violently disturbed by the submersible's bow wave. A dense population of small (approximately 50 mm long) specimens was found in one area during transect 5. This might have been a year-class of specimens, leading to the suggestion that this species might have an annual reproductive cycle.

Benthodytes sanguinolenta is much more reddish than the preceding species, and usually

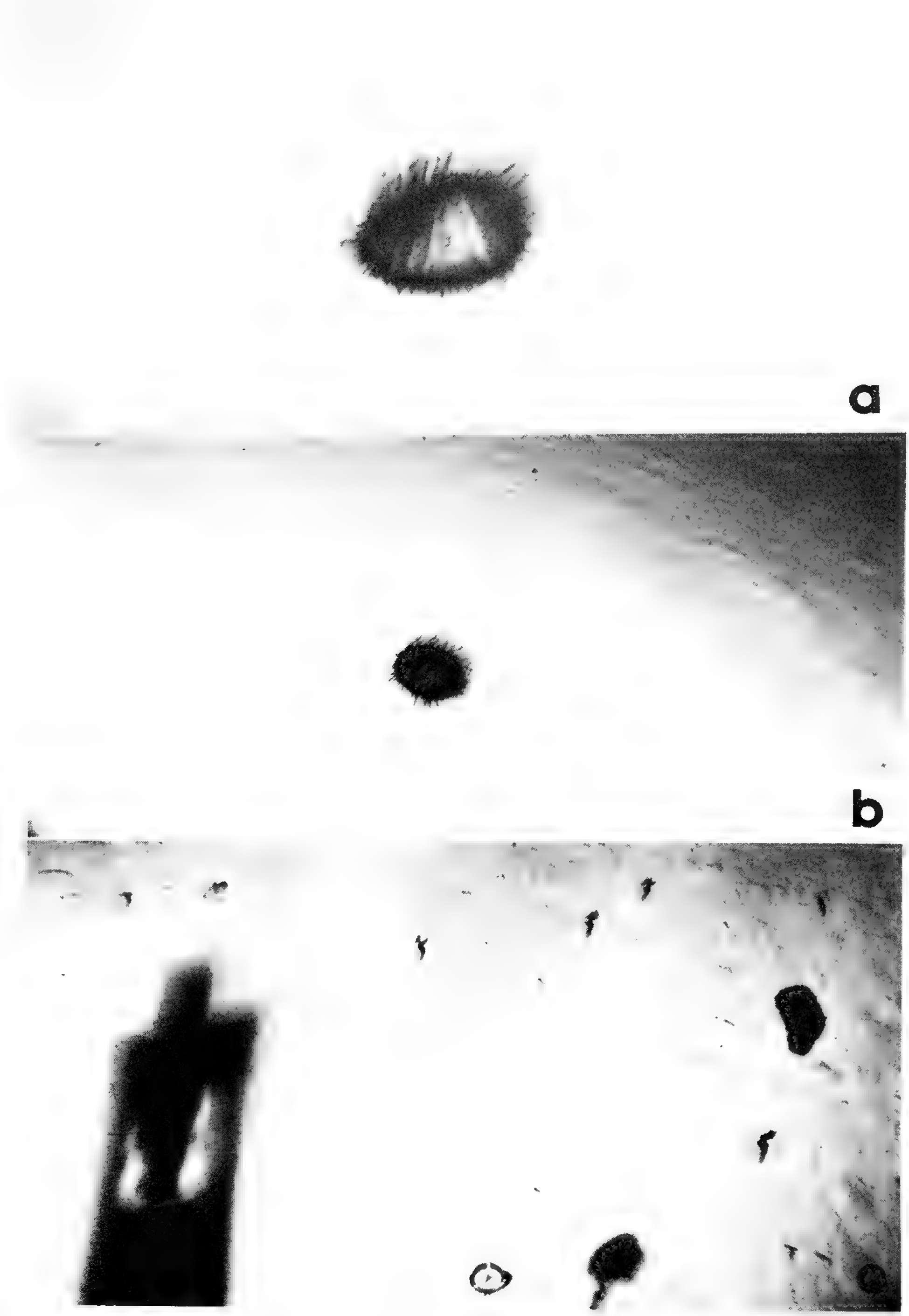

Fig. 2. Echinoids and holothurians. 2a, *Hygrosoma petersi* from *Alvin* Dive 592 (see text), with conspicuous hooves on oral spines. 2b, *Hygrosoma petersi* from *Alvin* Dive 703. Note that hooves are not visible, and that aboral spines are directed away from source of light (or from bow wave of submersible). 2c, six specimens of *Ellipinion delagei*, one of *Benthodytes lingua* (far right) and one of *Psychropotes depressa* (top left). Note that in this photo all specimens of *Ellipinion* are facing in the same direction.

considerably larger. Several specimens were observed to be swimming (figs 4a, b). Swimming movements were similar to those described for "*Euphronides* sp." (=*Psychropotes depressa* (Théel) according to Hansen (1975)) by Pawson (1976).

Benthodytes lingua is a large species, usually more than 30 cm long, uniformly light to dark violet (figs 1c, 2c). Specimens were relatively common in all transects and were among the most conspicuous invertebrates encountered during Dive 703. This species is apparently incapable of swimming.

Enypniastes eximia is common in the Tongue of the Ocean. The observations of Pawson (1976) can be enlarged upon here. Living specimens are light brown, translucent, and fragile. All but one of the specimens seen were swimming; some appeared to be drifting down towards the bottom passively, and others were ascending, gently undulating the anterodorsal veil. The mouth is apparently always directed upwards (figs 3a, b). All specimens observed swimming or floating past the viewing port were seen to have light coloured material of the same colour as the bottom sediments in their intestines. Eventually, a single specimen was found to be feeding on the seafloor (fig. 3c). The tentacles were very actively sweeping material in towards the mouth. We were unfortunately not able to determine the length of time that this specimen spent on the bottom, but judging by its active feeding rate, it would not need to remain there for more than a few minutes in order to fill its intestine. It seems likely that this species does rely on the seafloor for at least some of its food supply, and that it is not a permanent member of the nekton.

Paelopatides sp. was very common in some transects, especially numbers 5 through 8. Further identification of this species is impossible, regrettably, because the University of Miami collections did not include specimens of this fragile light pink species, which can reach a length of approximately 50 mm.

Pseudostichopus species A and B, and *Mesothuria verrilli* are often virtually indistinguishable through the viewing port of the submersible, because of their tendency to cover themselves with a layer of sediment (figs 4c, 5a). They were nowhere extremely common, but were conspicuous where they occurred because of their size (up to approximately 30 cm) and their conspicuous tracks. Systematic problems have necessitated a delay in making final identification of the two species of *Pseudostichopus*.

Freyella sp. is a six-armed brisingid asteroid which lies mouth down on the seafloor, with arms resting on the seafloor (Fig. 5c). This is an unusual feeding position for members of this family, for they usually raise their arms into the water column (Pequegnat et al., 1972, fig. W-1; Pawson, 1976, Pl. 3 figs. A-B). Maureen Downey of this Institution (personal communication) believes that this may be a new species of *Freyella*. A single specimen was collected by the *Alvin*, and it is now in the collections of the U.S. National Museum. The 11-armed *Freyella* sp. B was usually found on rocks, with its arms raised into the water column.

"*Luidia*" is a single specimen of five-armed asteroid which superficially resembled the genus *Luidia*. The arms were flattened, strap-like, and tapered gently from the small central disc to the bluntly pointed extremities. No specimens similar to this were found in the University of Miami collection.

Bathypectinura heros is a highly active uniformly orange ophiuroid, common in transects 1-4. It has been well described in two recent papers (Schoener, 1967; Madsen, 1973). Dr Daniel M. Cohen and I each saw a single individual of this species making active swimming movements in response to the approach of the submersible. In one case a specimen travelled a distance of approximately one metre by vigorously thrashing its arms. Maximum height above the seafloor was approximately one metre.

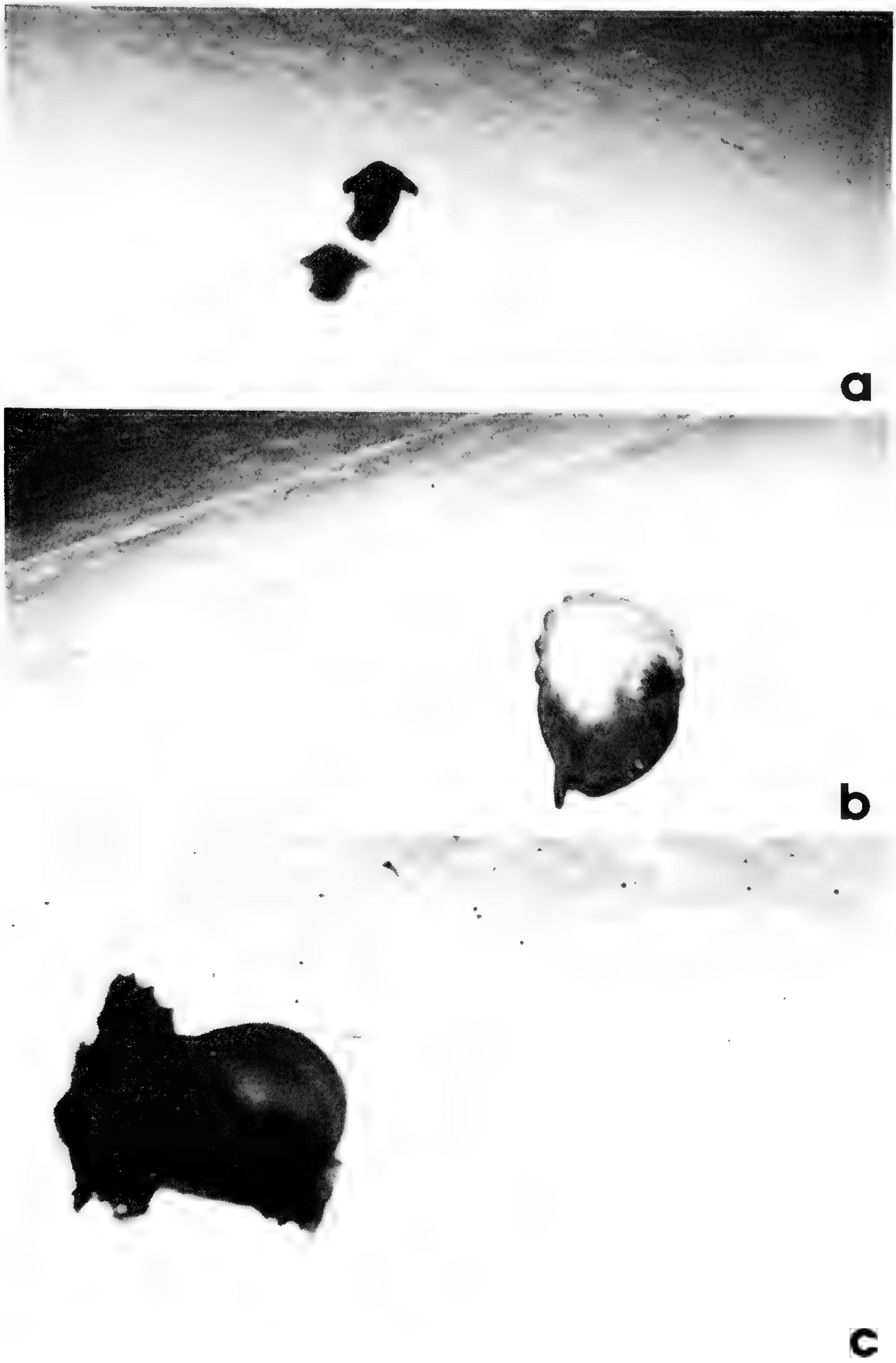

Fig. 3. The holothurian, *Enypniastes eximia*. 3a, specimen swimming, with gently undulating anterodorsal veil. 3b, another swimming specimen, showing mouth and tentacles. Photo, D. M. Cohen. 3c, a specimen on seafloor, actively feeding.

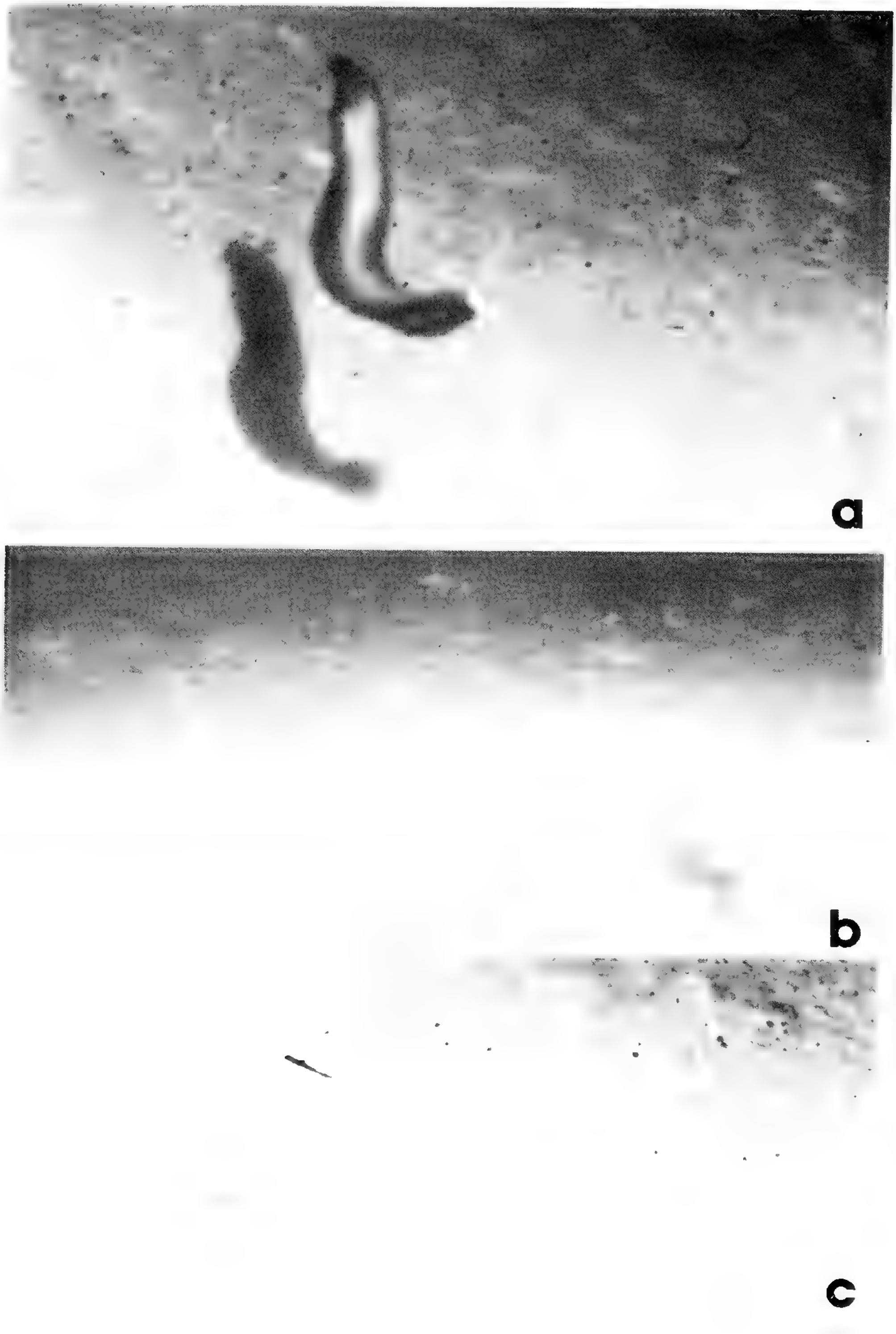

Fig. 4. Holothurians *Benthodytes* and *Mesothuria*. 4a, 4b, *Benthodytes sanguinolenta* swimming up and away from source of disturbance. 4c, *Mesothuria verrilli* on seafloor, with thin covering of sediment.

Ophiomusium species A and B have not yet been positively identified due to systematic problems. Barham et al. (1967), Grassle et al. (1975) and Wigley and Emery (1967) discuss behaviour and population densities of species of *Ophiomusium*.

"Red ophiuroid": this puzzling ophiuroid (fig. 5b) was seen in fairly large numbers during *Alvin* dives further north (see Cohen and Pawson, 1977). Regrettably, we were unable to collect any specimens of this brittle star. It is about the same size as *Ophiomusium lymani* with a light red disc, light orange-red arms and conspicuous red tube feet. Tongue of the Ocean specimens, like those observed further to the north, adopted a great variety of postures and also, presumably, feeding methods. Commonly, the animal lies mouth down on the seafloor with two or three arms raised into the water column. Several specimens were found occupying burrows (of their own making?) with two or three arms extended onto the seafloor surface. Others were more or less completely buried, with two or three arms projecting. A preliminary survey of University of Miami collections revealed no specimens which might represent this species, but a more detailed examination by a specialist is required.

6. FORMATION OF CONICAL MOUNDS ON THE SEAFLOOR

Several authors (Heezen and Hollister, 1971; Pequegnat et al., 1972, and others) have illustrated mounds of various kinds on the deep seafloor, and have suggested that the mounds are constructed by various burrowing organisms. It is well-known that some mounds with holes at their summits or with depressions near their bases are constructed by crustaceans or fishes. Other mounds, which are featureless, not associated obviously with other topographic features, have caused some puzzlement. During *Alvin* Dive 703 and other dives in the Tongue of the Ocean, several such mounds were disturbed mechanically by the movement of the submersible, and we were surprised to observe that in at least two cases the "core" of the mound consisted of a mass of holothurian faeces, such as may have been deposited by the genera *Ellipinion* or *Pseudostichopus*. Apparently the faeces, bound with some kind of mucus, act as a local surface feature upon which drifting and falling sediment can accumulate. In areas with little current activity, such mounds are almost perfectly symmetrical cones.

7. SHORT TRACKS ON THE SEAFLOOR

In numerous seafloor photographs, short holothurian tracks have been observed. These may begin and end within the field of the photograph, with no trace of the holothurian which made them. Two explanations may be offered to account for these tracks, and both involve swimming activities:

a. A swimming species landed on the seafloor, fed for a short distance, and then died, the dead animal eventually disappearing, leaving the track. Such a track may have been made very recently or perhaps hundreds of years ago, especially in areas were sedimentation rates are slow (Heezen and Hollister, 1971).

b. A swimming species landed on the seafloor, fed for a short distance, and then left again, perhaps to seek a more palatable sediment. During *Alvin* Dive 703, two specimens of *Benthodytes sanguinolenta* were seen to swim away, leaving short tracks behind them (fig. 1b). It is possible that a type of "trial and error" feeding is commonplace among the more mobile holothurians.

8. POPULATION DENSITIES OF ECHINODERMS

Counts of echinoderms in each transect (in numbers per 1000 m^2) are given in Table 2. For comparison, counts for another large invertebrate, the Venus flower basket sponge *Euplectella suberea* Thomson are also given. Some comments on distribution patterns follow. In view of the large scale sized used, it is not considered profitable to submit the figures given here to statistical

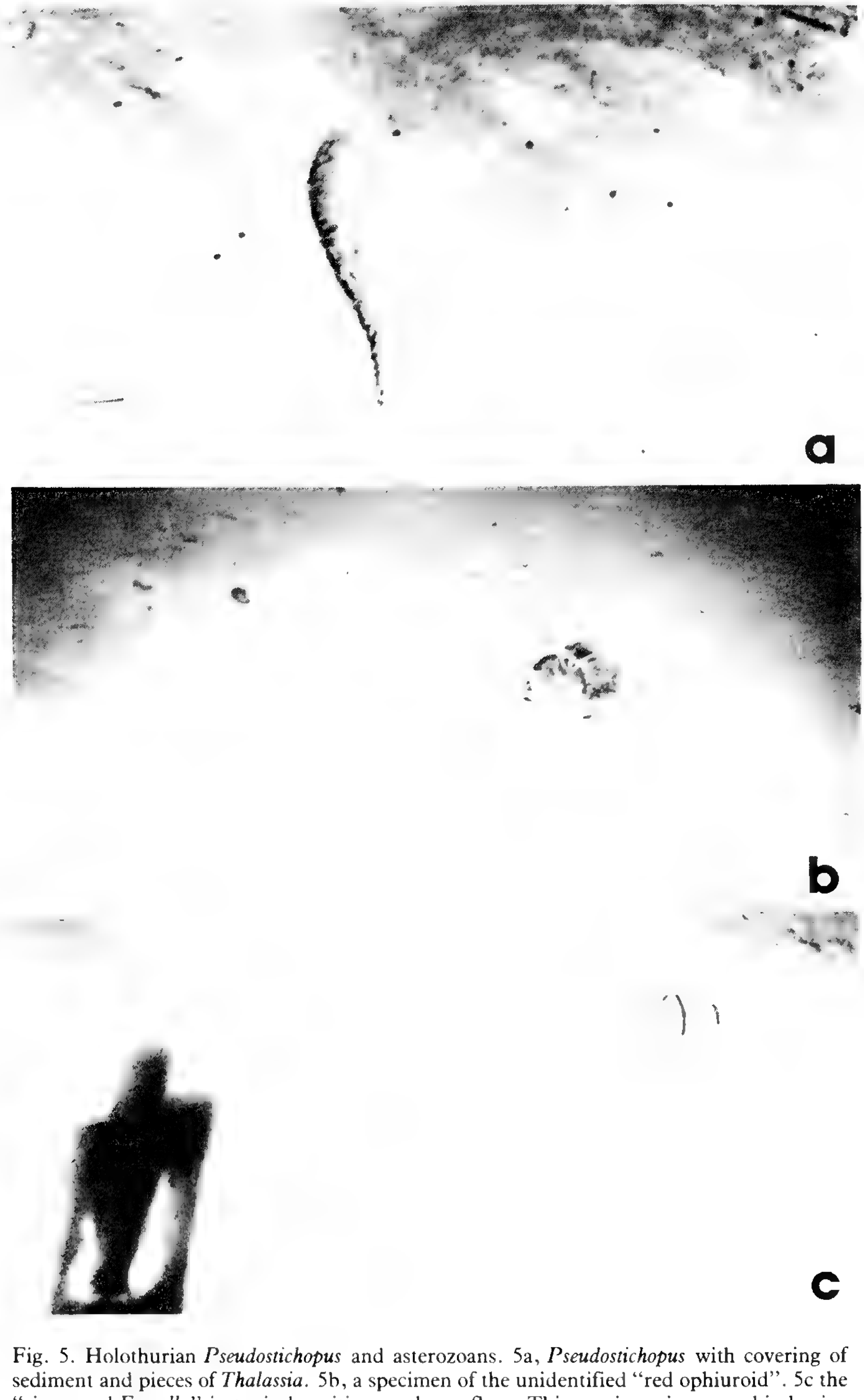

Fig. 5. Holothurian *Pseudostichopus* and asterozoans. 5a, *Pseudostichopus* with covering of sediment and pieces of *Thalassia*. 5b, a specimen of the unidentified "red ophiuroid". 5c the "six-armed *Freyella*" in typical position on the seafloor. This specimen is unusual in having seven arms.

tests for random *versus* non-random distribution patterns, such as were employed by Grassle et al. (1975) in their study of some deep-sea communities. However, it is believed that in spite of the limitations of the data, some inferences can be drawn which would seem to be reasonable in light of the data on feeding propensities presented elsewhere in this paper.

With a few exceptions, population densities were generally rather low. *Ophiomusium* spp. in transect 2, *Benthodytes typica sanguinolenta* in transect 5 and *Ellipinion delagei* in transect 7 approached densities of 1 per m^2, but apparently did not exceed them. By contrast, Grassle et al. (1975) found that *Ophiomusium lymani* in their study area (Dives 280 and 436) was far more numerous, reaching densities of 1.7 and 2.4 specimens per m^2 respectively. However, densities of other echinoderm species listed by Grassle et al. were relatively low, and tend to agree well with those given here.

a. Distribution patterns of "vegetarians": *Hygrosoma petersi*, which feeds on *Sargassum* and *Thalassia*, was more or less evenly distributed in all transects, except that there was a notable population increase in transect 7 followed by a sharp decline in transect 8. *Bathypectinura heros*, by contrast, reached relatively high numbers during transects 1-4, and was virtually absent from all subsequent transects except transect 8. Note that the increase in this last transect is matched by a decline in numbers of *Hygrosoma petersi*.

Although the Sargassum-Thalassia fragments are ubiquitous, it appears that the two species discussed above are not evenly scattered on the seafloor, and that there may be some evidence here of competitive exclusion, involving other species of echinoderms, or other invertebrates.

b. Distribution patterns of "mud-ball swallowers": *Phormosoma placenta* was unevenly distributed over all transects, reaching peaks in transects 1, 2 and 7. *Plesiodiadema antillarum* and *Salenocidaris profundi* were common in the first four transects and then dropped out altogether. Perhaps the latter two species are more selective in their feeding and the endpoint of transect 4 might represent the local southern limit of the "range" of their desirable food resource. No herds of *Phormosoma* like those described by Grassle et al. (1975) were found in the Tongue of the Ocean. Specimens were rather widely scattered.

c. Distribution patterns of "non-selective" mud swallowers: While most deep-sea holothurians might be classed as non-selective in their feeding habits, undoubtedly they continually move to areas of higher nutrient content for their feeding, in the same manner as do their shallow-water counterparts. Table 2 shows that several species are present in relatively low numbers in several transects, and then over a few transects population counts rise dramatically. The two species of *Benthodytes* achieved such high densities in transect 5 that it was impossible to count them with any degree of accuracy. *Ellipinion delagei* reached a peak in transect 7, and by transects 10 and 11 had disappeared completely. *Psychropotes depressa* and *Benthodytes lingua* also reached peak populations in transect 7, but in contrast to *Ellipinion delagei* these species were also well represented in transects 10 and 11.

Paelopatides sp. shows a pattern similar in many respects to that of *Psychropotes depressa* and *Benthodytes lingua*, except that the peaks for the first species were reached in transects 6 and 7, while for the latter two species there was a sharp increase in numbers from transect 6 to transect 7. *Mesothuria verrilli* and *Pseudostichopus* A and B were more or less evenly distributed over all transects, their numbers dropping slowly towards the last transect runs.

Examination of intestine contents of several of the species discussed above revealed no obvious differences at the gross level. A study of organic content of sediments in the various transect areas might be useful. Sanders et al. (1965) found that for the Gay Head — Bermuda study, distribution of animals on the seafloor was not obviously correlated with organic content of the sediment. This negative result was ascribed to an inadequacy in the analytical techniques

used. Clearly, further study of this topic is required.

It is evident from Table 2 that two important population peaks for mud-swallowers were reached in different transects. The first, in transect 7, includes *Ellipinion delagei*, *Psychropotes depressa* and *Benthodytes lingua*, while the second comprises *Benthodytes typica* and *B. sanguinolenta*.

Differing nutritional requirements, competition, aggregation as a result of social behaviour might be suggested as causes for staggering of population peaks for the various feeding categories discussed above. Contagious distributions have been noted in deep-sea echinoderms on several occasions (see Grassle et al., 1975). The phenomenon of social behaviour in echinoderms has received some attention recently (Pearse and Arch, 1969; Grünbaum et al., 1978), and it is possible that the obvious "clumping" of deep-sea species discussed here is the result of some social interaction that is not yet understood. In some cases, the aggregation is clearly related to distribution of food resources, as shown by Pawson (1976) for a species of *Scotoplanes*, but for the most part, no obvious explanations are forthcoming.

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9. A BIOMETRICAL STUDY OF POPULATIONS OF THE EUROPEAN SEA-URCHIN *ECHINUS ESCULENTUS* (ECHINODERMATA: ECHINOIDEA) FROM FOUR AREAS OF THE BRITISH ISLES

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SUMMARY

Results submitted by mainly amateur diving groups during Underwater Conservation Year 1977 in the United Kingdom show that there are regional differences in the relationship between both size and shape of specimens of the European sea-urchin *Echinus esculentus* Linnaeus and the depth at which they occur. Populations from South-West England are significantly bigger at all depths than those from the other areas surveyed, those from Western Scotland increase in size more rapidly with increasing depth of water, and those from the North Sea decrease in size with increasing depth. Two sites surveyed in South-West Ireland show that exposure may affect the size of urchins inhabiting shallow waters. The results are compared with those of a similar survey by Larsson (1968) on the same species in Swedish waters.

INTRODUCTION

The European sea-urchin, *Echinus esculentus* Linnaeus, was the subject of a nationwide survey during 1977 as part of a special project for amateur divers during Underwater Conservation Year (UCY 77) in the United Kingdom. The project was timely, since there has been unsupported evidence over the past few years that populations of the animal have been suffering at the hands of collectors for the curio trade (see, for instance, Natural Environment Research Council, 1973). It is possible that the animal may also become the subject of additional pressure from the luxury food trade, since the roe is considered a delicacy by some (Southward and Southward, 1975). In addition, there is contradiction in the results of previous studies that have examined the population structure of this animal in European seas: Moore (1935) and Reid (1935), working on dredged material from the Isle of Man and Scotland, both state that the largest urchins inhabit shallow water, while Larsson (1968), who used SCUBA techniques to study populations in the Koster Fjord region of Sweden, found larger specimens in deeper water.

Studies of extensive populations, and over a wide geographical area, require larger teams of investigators than are usually available in the normal course of scientific work, and for this reason the opportunity to use the diving expertise of competent amateurs during a year of special effort was welcomed. Before the start of the project, standardised instructions were prepared which outlined in straightforward terms the procedures to be adopted. Several different observational and experimental projects were suggested (Nichols, 1978a), and this paper describes the results of one, an investigation of the size and shape of the urchins relative to the depth of water at which they live.

METHODS

Details of the instructions sent out to diving groups prior to the start of the project are given in Nichols (1979). Diving groups were advised to construct a simple pair of calipers with which the two dimensions of diameter and height could be taken on the animal while underwater and read off along the side of a recording board. Since this was also a conservation exercise, a more elaborate design of calipers was suggested to some teams which obviated the need to disturb the urchins, even when taking the *height* measurement.

Teams were asked to record the measurements of all urchins encountered within a convenient area at any depth. Where possible, depth gauges were calibrated or corrected in pressure chambers, and all depth readings were corrected to Lowest Astronomical Tide. The surveys were conducted within four months of each other (Table 1). Results were transferred to a standard form for return to the project co-ordinator, and data were processed using a desk computer to provide standard statistical treatment.

In his study of a Swedish population of the same species of sea-urchin in 1966, Larsson recorded only the diameter of individual urchins and plotted this dimension against depth of water as a histogram (see Larsson, 1968, fig. 15). The time of year that Larsson made his survey is not given. These results have been replotted in the present paper in a comparable form to those of the British specimens and standard statistical treatment applied to them.

RESULTS

Of the total results submitted, those from four localities have been selected for the purposes of this paper, to provide as wide a geographical spread around the British Isles as possible (Fig. 1). Details of the sites in each area, the survey teams and the numbers of urchins measured in each case are given in Table 1. The test dimensions of *diameter* and *height* are plotted separately for each site, and the *ratio* of height to diameter also plotted on a separate axis on the same graph (figs 2 to 4).

Table 1. Summary of the surveys included in this paper.

Location	Survey team and Leaders	Dates	No. of urchins measured	
1. W. Scotland, Isle of Skye	Army Air Corps, Middle Wallop, Sub-Aqua Club Sgt. R. Perren	10-24 August 1977	a. Black Is	103
			b. Crowlin Is	84
			c. Eilean Ban	107
			d. Eileanan Dubha	255
			e. Tulm Is	154
			Total	703
2. S. W. England, Lamorna Cove	University of Exeter Sub-Aqua Club Deborah Garner Andrew Smith	30 June to 8 July 1977		151
3. S. W. Ireland, Bantry Bay	University of Cambridge Sub-Aqua Club Alasdair Edwards Alison Morris	16 June to 17 July 1977	i. Carrigavaddra	504
			ii. Sheelane Is	504
			Total	1008
4. North Sea, St. Abb's and Newton	University of Durham Sub-Aqua Club Christine Howson Charles Anderson	8 May to 16 June 1977		40

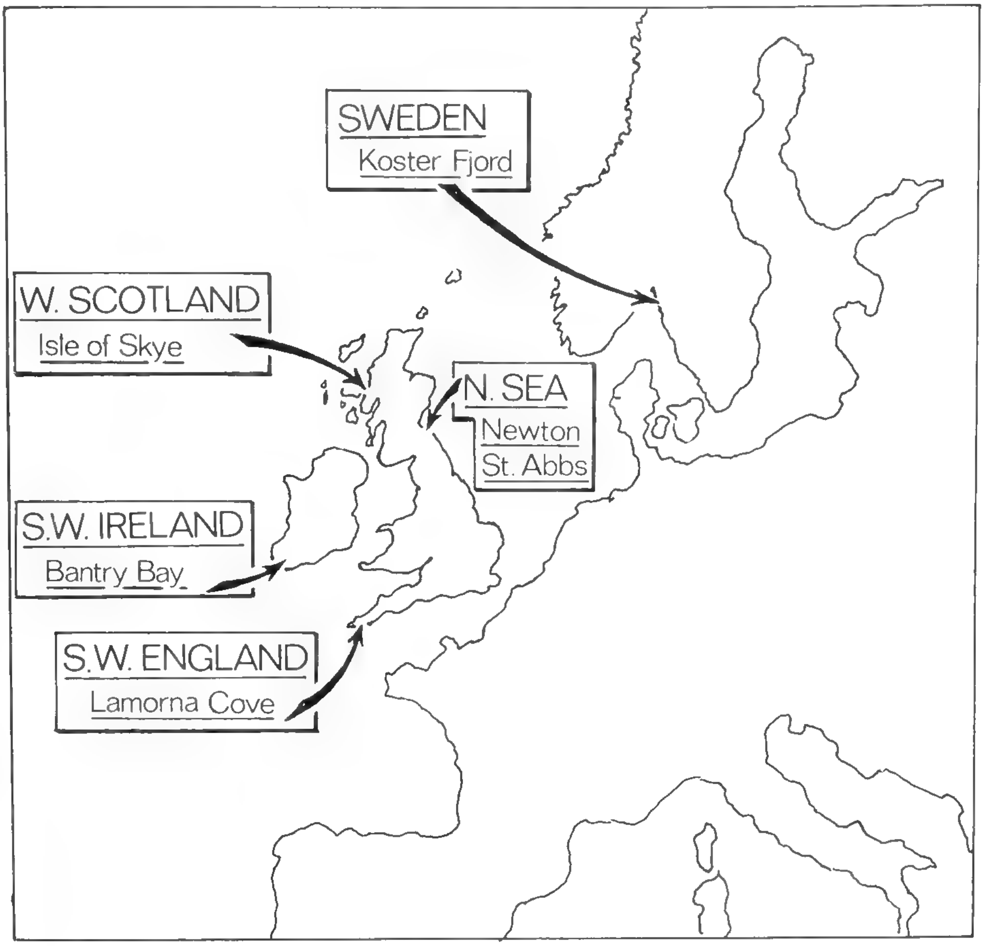


Fig. 1. Map of part of Europe, to show the location of the four areas around the British Isles surveyed in this study, and the location of the area in Sweden surveyed by Larsson in 1966.

Figure 2 shows a summary of results from five separate sites in Western Scotland; four of the sites were within a radius of 5 km, while the fifth, Tulm Island, was about 30 km away from the main group of sites. Figure 2f plots the mean values for all five sites. Confidence limits (standard errors) are included as vertical bars about the mean values at each depth, where these limits extend beyond the size of the symbols. In each case linear regressions of best fit are drawn through the points.

The graphs in figure 2 show that for all sites in Western Scotland the dimensions of diameter and height increase with depth of water, and there is no significant difference between rate of increase in the two dimensions except in the case of Tulm Island (fig. 2e). So far as the ratios of the two dimensions are concerned, Tulm Island (fig. 2e) is the only one to show a negative slope, meaning that at this site alone the animals may become squatter in deeper water. However, it must be added that only two animals were measured at each of the depths 17 and 18 m, and without the results from these small samples the regression for the ratio, like the others, shows a positive slope.

In South-West Ireland (fig. 3), two sites were surveyed. The one (Carrigavaddra) was

Fig. 2. Graphs showing the relationship between mean dimensions (diameter, open circles; height, open triangles) and depth of water in which they occur of populations of the sea-urchin *Echinus esculentus* from five separate sites near the Isle of Skye, Western Scotland (a to e), and the mean values for all sites (f). The mean values for the ratio of height to diameter for each individual are plotted (solid squares) on the same graphs, the left-hand axis being the dimensions and the right-hand axis being the ratio in each case. Calculated linear regressions are drawn in as solid lines, and the confidence limits (standard error) are drawn as vertical lines about the mean values where these limits extend beyond the symbols.

Regression equations are as follows:

a.	Black Island.	Diameter:	$y = 7.38 + 0.15x$
		Height:	$y = 4.60 + 0.18x$
		Ratio:	$y = 0.64 + 0.0073x$
b.	Crowlin Island.	Diameter:	$y = 6.47 + 0.264x$
		Height:	$y = 4.55 + 0.269x$
		Ratio:	$y = 0.57 + 0.017x$
c.	Eilean Ban.	Diameter:	$y = 7.04 + 0.245x$
		Height:	$y = 5.27 + 0.237x$
		Ratio:	$y = 0.74 + 0.007x$
d.	Eileanan Dubha.	Diameter:	$y = 7.81 + 0.036x$
		Height:	$y = 5.17 + 0.077x$
		Ratio:	$y = 0.63 + 0.01x$
e.	Tulm Island.	Diameter:	$y = 6.13 + 0.345x$
		Height:	$y = 5.44 + 0.209x$
		Ratio:	$y = 0.83 - 0.004x$
f.	Mean of all sites.	Diameter:	$y = 7.05 + 0.176x$
		Height:	$y = 4.91 + 0.182x$
		Ratio:	$y = 0.69 + 0.007x$

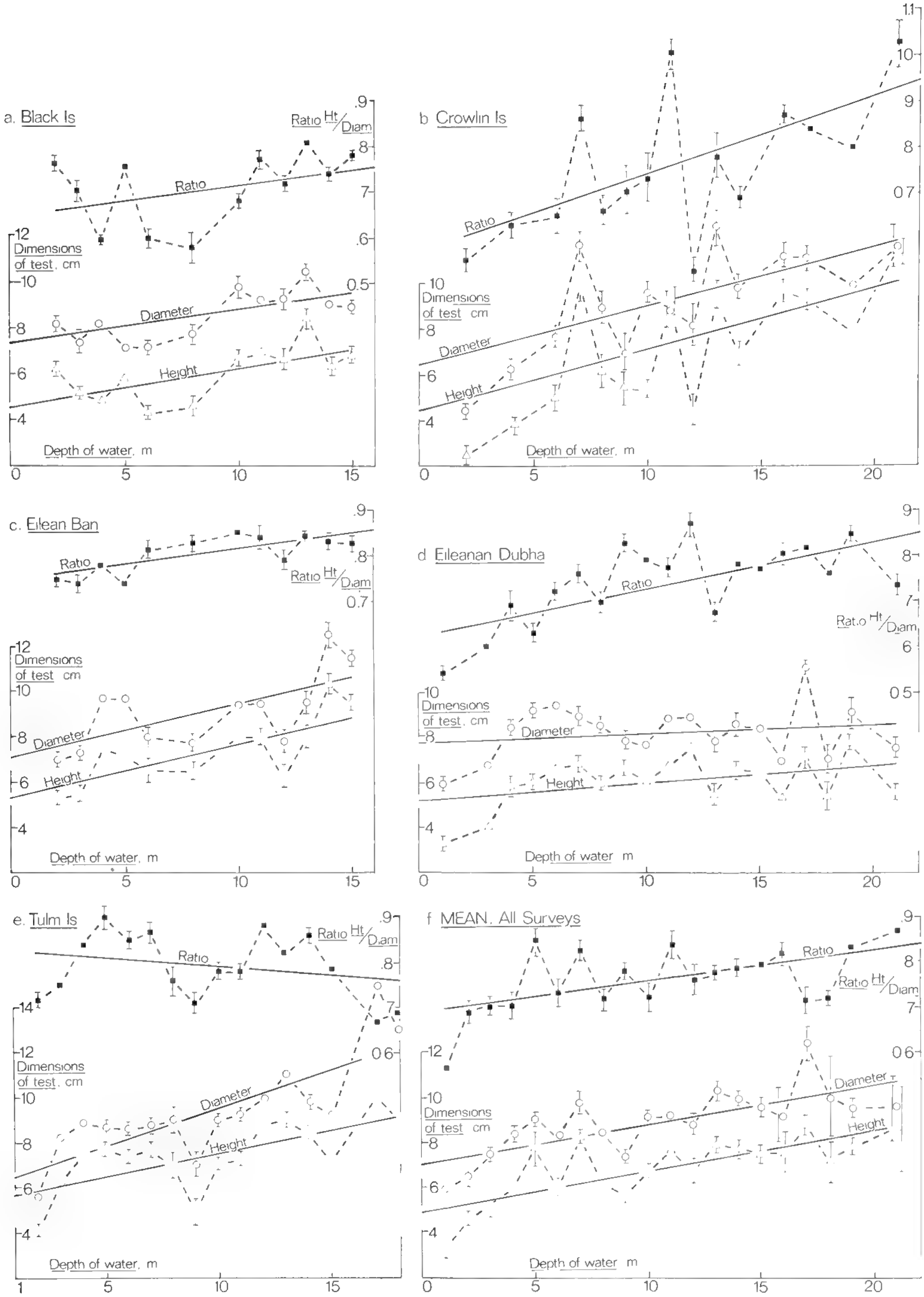

a. Black Is
Ratio Ht/Diam
Ratio
Dimensions of test, cm
Diameter
Height
Depth of water, m
b Crowlin Is
c. Eilean Ban
d Eileanan Dubha
e. Tulm Is
f MEAN, All Surveys

Fig. 3. Graphs showing the relationship between mean values of diameter, height and ratio to depth of water for specimens of *Echinus esculentus* from two sites in Bantry Bay, South-West Ireland. Conventions as for Figure 2.

Regression equations are as follows:

a.	Carrigavaddra.	Diameter:	$y = 8.45 + 0.031x$
		Height:	$y = 6.52 + 0.047x$
		Ratio:	$y = 0.768 + 0.003x$
b.	Sheelane Island.	Diameter:	$y = 8.013 - 0.012x$
		Height:	$y = 6.078 + 0.010x$
		Ratio:	$y = 0.762 + 0.0025x$

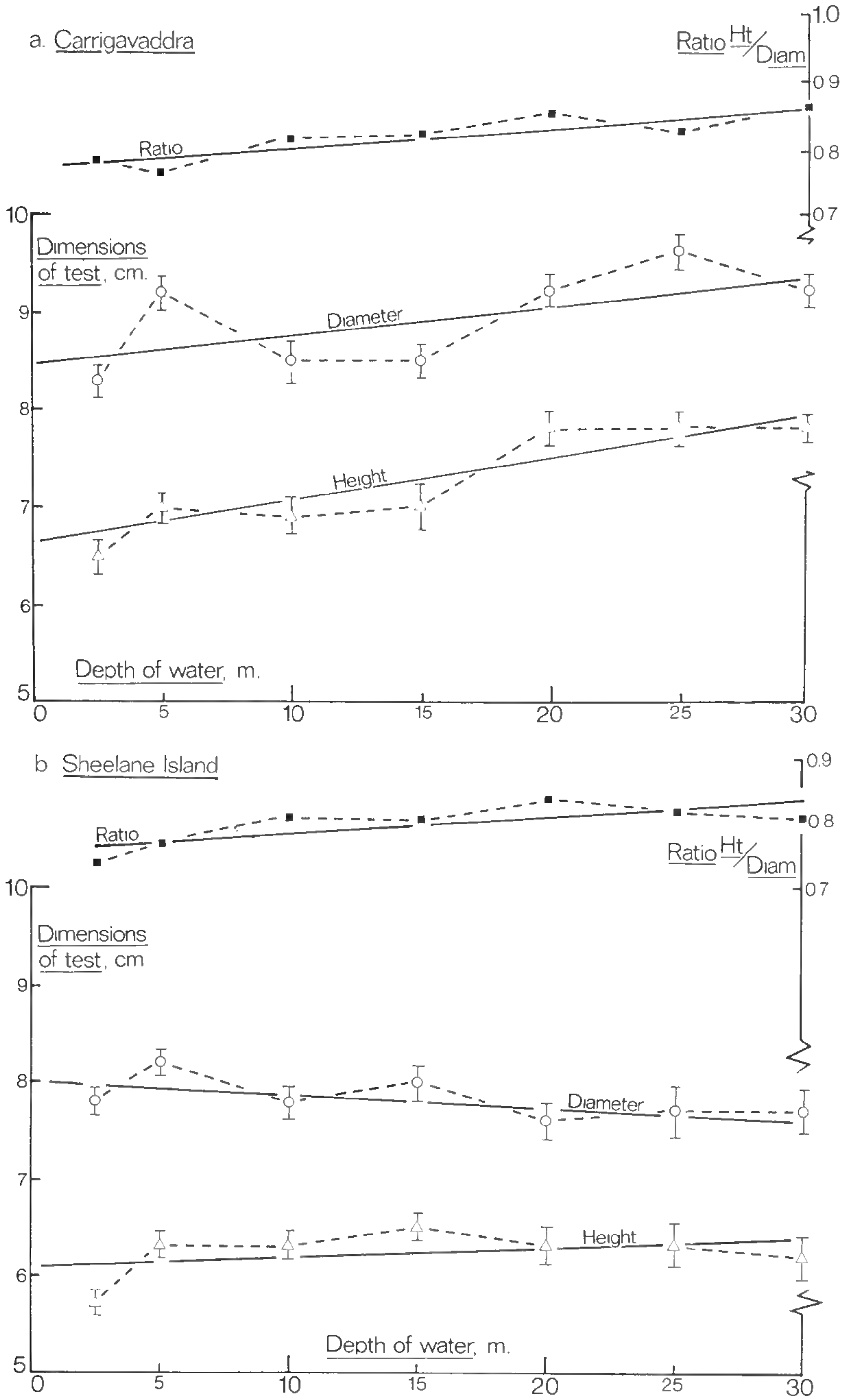
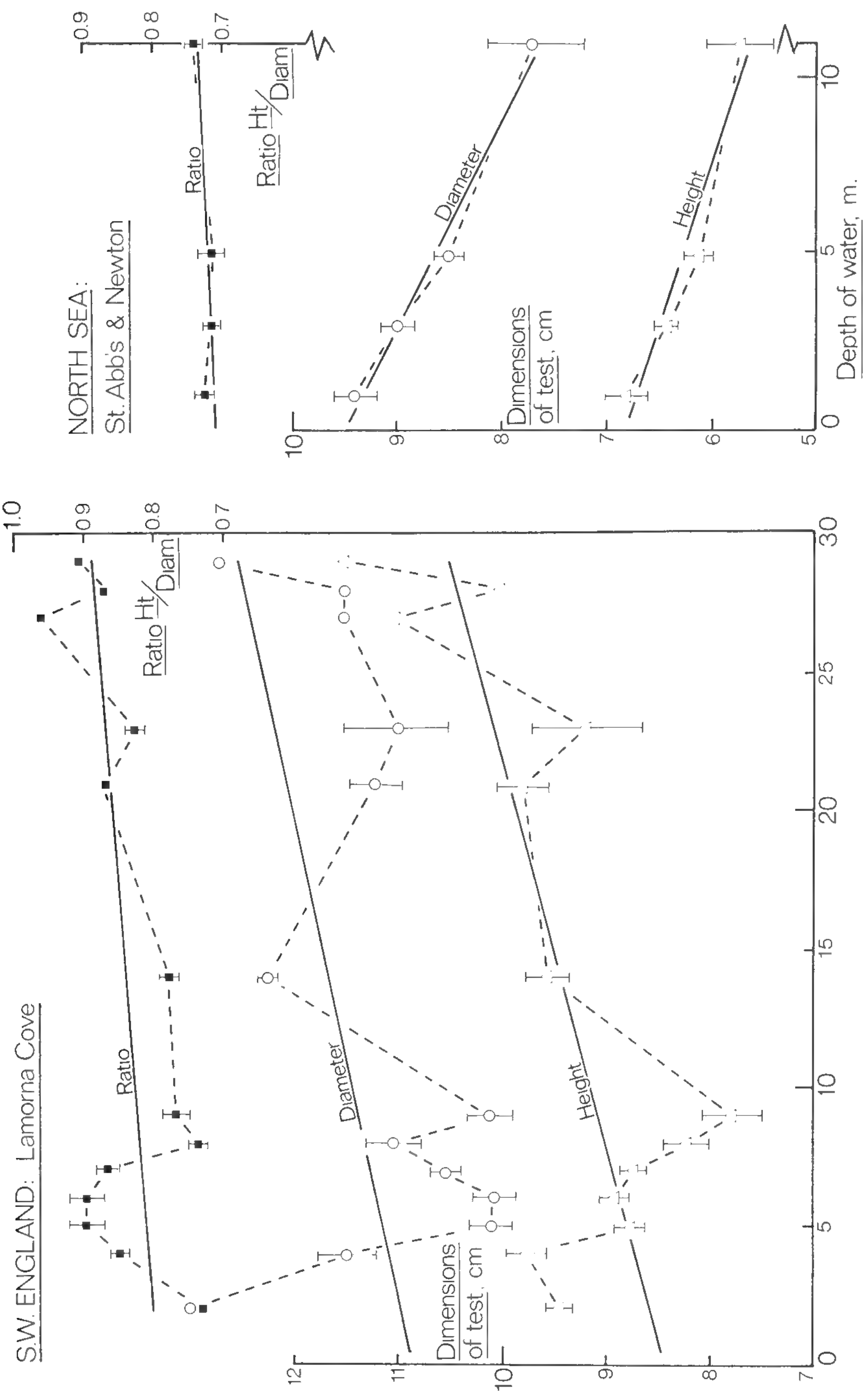

a. Carrigavaddra
Ratio Ht/Diam
1.0
0.9
0.8
0.7
Ratio
Dimensions of test, cm.
10
9
8
7
6
5
Diameter
Height
Depth of water, m.
0
5
10
15
20
25
30
b Sheelane Island
0.9
0.8
0.7
Ratio
Ratio Ht/Diam
Dimensions of test, cm
10
9
8
7
6
5
Diameter
Height
Depth of water, m.
0
5
10
15
20
25
30

Fig. 4. Graphs showing the relationship between mean values of diameter, height and ratio for specimens of *Echinus esculentus* from a. Lamorna Cove, South-West England, and, b. St. Abb's and Newton, on the North Sea coast of Britain. Conventions as for Figure 2.

Regression equations are as follows:

a.	South-West England.	Diameter:	$y = 10.88 + 0.033x$
		Height:	$y = 8.433 + 0.071x$
		Ratio:	$y = 0.797 + 0.003x$
b.	North Sea.	Diameter:	$y = 9.49 - 0.168x$
		Height:	$y = 6.768 + 0.104x$
		Ratio:	$y = 0.712 + 0.0021x$


NORTH SEA:
St. Abb's & Newton
Ratio
Ratio Ht/Diam
Diameter
Height
Dimensions of test, cm
Depth of water, m.
SW. ENGLAND: Lamorna Cove
Ratio
Ratio Ht/Diam
Diameter
Height
Dimensions of test, cm

towards the seaward end of a long, narrow inlet (Bantry Bay), while the other (Sheelane Island) was at a slightly more sheltered site further into the Bay. The results for Carrigavaddra (fig. 3a) are similar to the mean result from Western Scotland (fig. 2f), while those for Sheelane Island (fig. 3b) show that here the average diameters of the urchins measured decreased with depth of water, and the average heights increased. At both sites the ratios show a positive slope, that is, on average the urchins are becoming taller with depth.

In South-West England the site chosen was at Lamorna Cove, Cornwall, a fairly exposed site. The results (fig. 4a) show that here again diameter and height, and the tallness of the urchins, increase with depth of water.

The last area consisted of two sites near the English-Scottish border on the North Sea coast of the United Kingdom. This area yielded the least satisfactory set of results, because the North Sea between the British Isles and Scandinavia is more turbid than other waters from which surveys were taken, and few populations of the sea-urchin occur here. The two sites are about 30 km apart; the one at Newton-By-Sea, in the English county of Northumberland, has populations of urchins at depths of between 1 and 5 m, while the other, at St. Abb's, in the Scottish county of Berwickshire, has populations at 11 m depth. The results (fig. 4b) are combined, despite their slightly separated provenance. The graph shows that this area may be different from the others here described, in that both diameter and height decrease with depth of water; the tallness, however, increases. However, it must be noted that the sample size in this case is somewhat smaller than the others.

The calculated mean linear regressions for diameter, height and ratio for the four British Isles areas are summarised in figure 5. Where more than one site in each area has been surveyed, as in Western Scotland (5 sites) and South West Ireland (2 sites), the means of all sites in that area are plotted here, to show regional differences, if any. The lower part of the figures shows the diameters (upper line of each quadrilateral) and height (lower line) and the depth range for each of the surveyed areas; the upper part of the figure shows the mean ratios for the four areas. The figure shows that the urchin populations from South-West England are significantly different from those of the other areas, in that both the overall size at all depths is larger, and they have taller tests at all depths. Other differences that are revealed by this figure are that the rate of increase in size with depth and the increase in tallness with depth for urchins from Western Scotland are both greater than for other areas, and that the small and shallow sample from the North Sea shows that here the urchins decrease in size with depth of water.

Not all survey teams that contributed to this project were able to dive to the depths to which *Echinus* extends. Indeed, in some areas, such as the North Sea, the urchins themselves do not extend to any great depth, at least in the area surveyed. At some sites too, rather few specimens were encountered in deeper water, so the inclusion of the deepest results may be to some extent unjustified. To make a fairer comparison, the linear regressions for all sites down to a depth of 15 m only have been summarised in figure 6. In fact, the general statements above about the separation of the various areas hold true for these restricted results too. But there are minor differences. For instance, for populations in South-West England, omission of the deeper specimens shows that the regressions for both diameter and height (top and bottom lines for the 'South-West England' quadrilateral in figure 6) now show negative slopes, that is, the specimens become marginally smaller with depth. The ratio (tallness) for this area (upper part of the figure) also now shows a negative slope, though there is no significant difference between this line and a constant ratio (horizontal line) ($P>0.5$).

Larsson's (1968) paper included only diameters of the specimens he measured from the Koster Fjord, Sweden, in 1966. These results have been plotted on the same axes as the results here described from the British Isles (fig. 7). This graph shows that the Swedish population

structure for this urchin is very different from that from all the British sites; in particular, the urchins in shallow water have a much smaller mean size, though the ranges overlap somewhat in deeper populations. It should be mentioned that Larsson's results and those reported here are separated by 11 years, but variation in individual sizes with time to the extent seen in these sets of results is unlikely, and in any case cannot be tested until the results from either country are repeated in the future.

DISCUSSION

In this paper, trends in the size and shape of the components of the populations with changing depth of water are indicated by plotting linear regressions of the mean values of each depth for the two dimensions of diameter and height of the animal's body and also that of mean values at each depth of the ratio between these two dimensions for each individual. It is insufficient to rely solely on the regressions for diameter and height to express shape. For instance, in cases where the regressions for diameter and height lie approximately parallel to one another, as for Crowlin Island, Western Scotland (fig. 2b), this does not necessarily mean that the tallness of the animal remains constant throughout the depths surveyed; indeed, in this example the regression for the ratio of height to diameter has a markedly positive slope, showing that the average tallness of the animals at this site increases significantly with depth.

There is little substantial difference between results for the sites surveyed in Western Scotland, so far as the calculated linear regressions reveal the trends. Black Island, Crowlin Island, Eilean Ban and Eileanan Dubha (fig. 2, a to d) are all strikingly similar. The somewhat different results obtained from Tulm Island (fig. 2e) are more apparent than real, in that the regressions are skewed because of the inclusion of results from small samples (2 urchins only at each) from 17 and 18 m depth. In particular, the line for the ratio of height to diameter shows a negative slope. If results from these two small samples are omitted, the linear regressions show slopes that are similar to those for all the other Scottish sites.

The two sites surveyed in South-West Ireland differ from each other in that the one (Carrigavaddra) is nearer the open sea, and therefore more exposed, than the other (Sheelane Island), which is about half way up the elongated bay. This may account to some extent for the differences between the regressions for diameter and height, the urchins being relatively smaller inshore at Carrigavaddra, but larger inshore at Sheelane. Perhaps this reflects the exposure of the area in which they live, since a larger urchin is more likely to be displaced in the rougher waters of the exposed site.

The site in South-West England, Lamorna Cove (fig. 4a) is remarkable for a drop in the average size of urchins between about 5 and 10 m depth of water. This could be explained by some factor, such as the substratum, affecting the general success of the urchins at these depths, though nothing was reported by the diving team; or alternatively it could be a factor related to predation. It happens that this site is a favourite one for the collection of urchins by amateur divers for the curio trade (Nichols, 1978b). Such divers normally descend to between 5 and 10 m depth so that the dive can be recorded in their log-books, and it seems quite likely that the activities of these people have denuded the populations of the larger urchins at these depths.

The results from the North Sea sites, combined on one graph (fig. 4b), are the least satisfactory in this study; although they show an unequivocal trend towards a reduction in size in deeper water, this cannot be supported with confidence on these small and separated populations. The shape of the urchins from both sites appears to remain almost unchanged in the 10 m depth through which the animals occur.

A comparison of all four areas surveyed around the British Isles, as shown on the summary

Fig. 5. Summary graph of means of all results from each of the four areas of the British Isles surveyed in this investigation. In the lower part of the figure the top line of each quadrilateral is the regression for the mean values of the diameters of sea-urchins over the depth range surveyed, and the lower line is the regression for the mean values of the heights. In the upper part of the figure, the regressions for the mean values of the ratio of height to diameter against depth of water are plotted. Left-hand axis represents the dimensions and right-hand axis the ratios.

Regression equations are as follows:

South-West England.	Diameter:	$y = 10.88 + 0.033x$
	Height:	$y = 8.43 + 0.071x$
	Ratio:	$y = 0.797 + 0.0033x$
Western Scotland.	Diameter:	$y = 7.051 + 0.176x$
	Height:	$y = 4.91 + 0.182x$
	Ratio:	$y = 0.688 + 0.007x$
South-West Ireland.	Diameter:	$y = 8.23 + 0.009x$
	Height:	$y = 6.301 + 0.029x$
	Ratio:	$y = 0.769 + 0.0025x$
North Sea.	Diameter:	$y = 9.49 - 0.168x$
	Height:	$y = 6.768 - 0.104x$
	Ratio:	$y = 0.712 + 0.0021x$

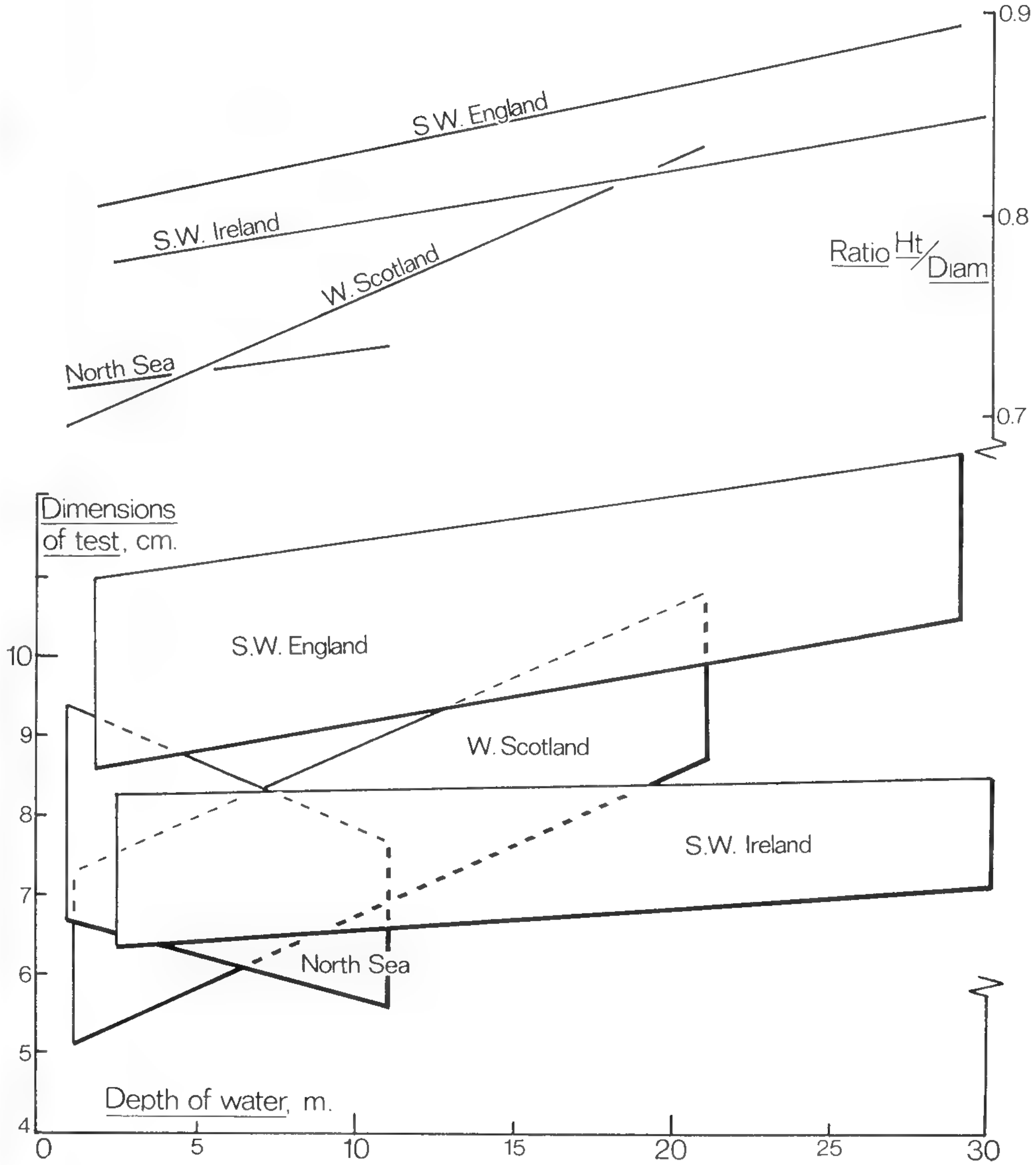
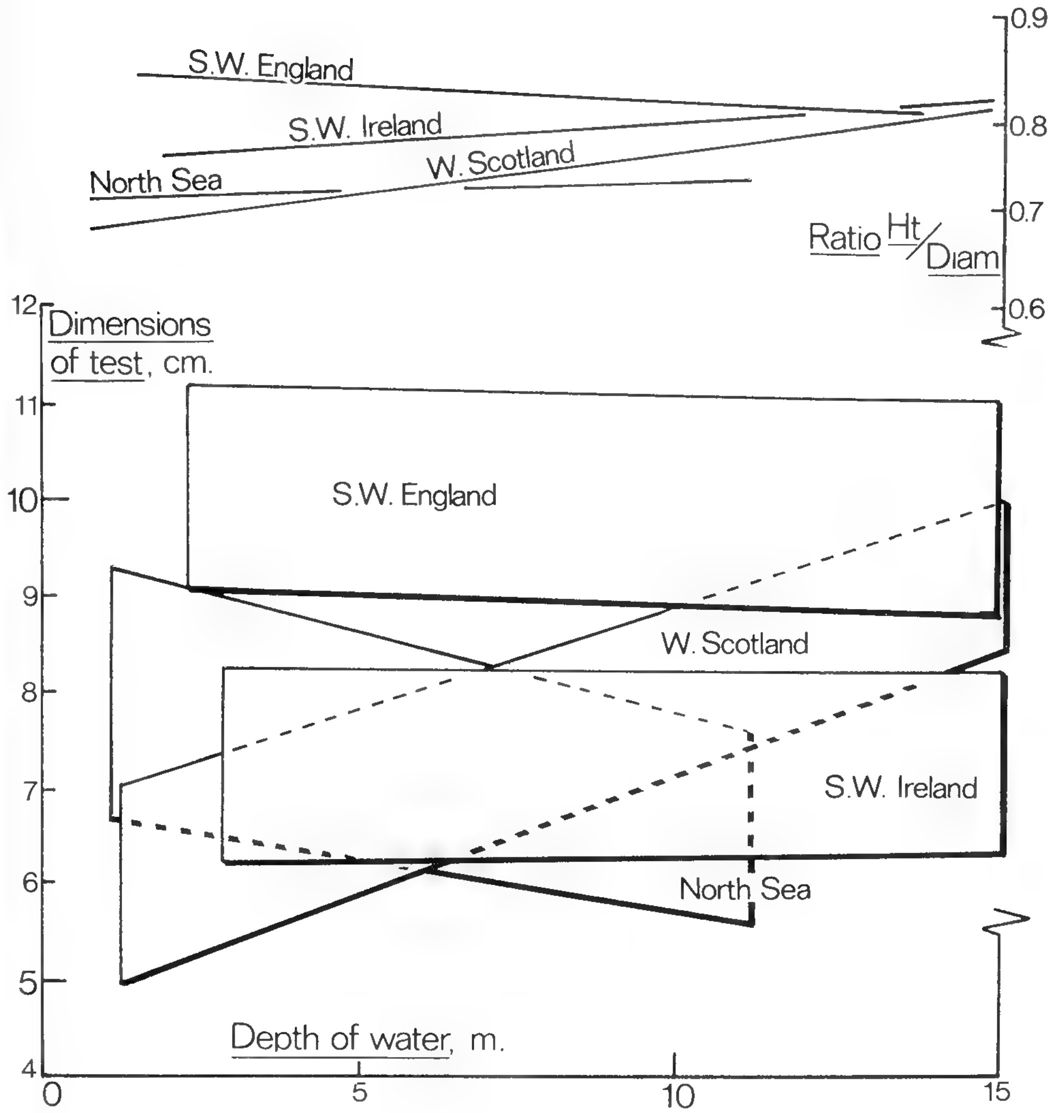

0.9
0.8
0.7
S.W. England
S.W. Ireland
W. Scotland
North Sea
Ratio Ht/Diam
Dimensions of test, cm.
S.W. England
W. Scotland
S.W. Ireland
North Sea
10
9
8
7
6
5
4
Depth of water, m.
0
5
10
15
20
25
30

Fig. 6. Summary graph of means of results from each of the four areas of the British Isles surveyed in this investigation, but ignoring all results from below 15 m depth of water. Conventions as for Figure 5.

Regression equations are as follows:

South-West England.	Diameter:	$y = 11.21 - 0.019x$
	Height:	$y = 9.159 - 0.038x$
	Ratio:	$y = 0.843 - 0.004x$
Western Scotland.	Diameter:	$y = 6.75 + 0.219x$
	Height:	$y = 5.64 + 0.227x$
	Ratio:	$y = 0.673 + 0.0095x$
South-West Ireland.	Diameter:	$y = 8.33 - 0.005x$
	Height:	$y = 6.20 + 0.04x$
	Ratio:	$y = 0.748 + 0.0051x$
North Sea.	Diameter:	$y = 9.49 - 0.168x$
	Height:	$y = 6.768 - 0.104x$
	Ratio:	$y = 0.712 + 0.0021x$


S.W. England
S.W. Ireland
W. Scotland
North Sea
0.9
0.8
0.7
0.6
Ratio Ht/Diam
12
Dimensions of test, cm.
11
10
9
8
7
6
5
4
S.W. England
W. Scotland
S.W. Ireland
North Sea
Depth of water, m.
0
5
10
15

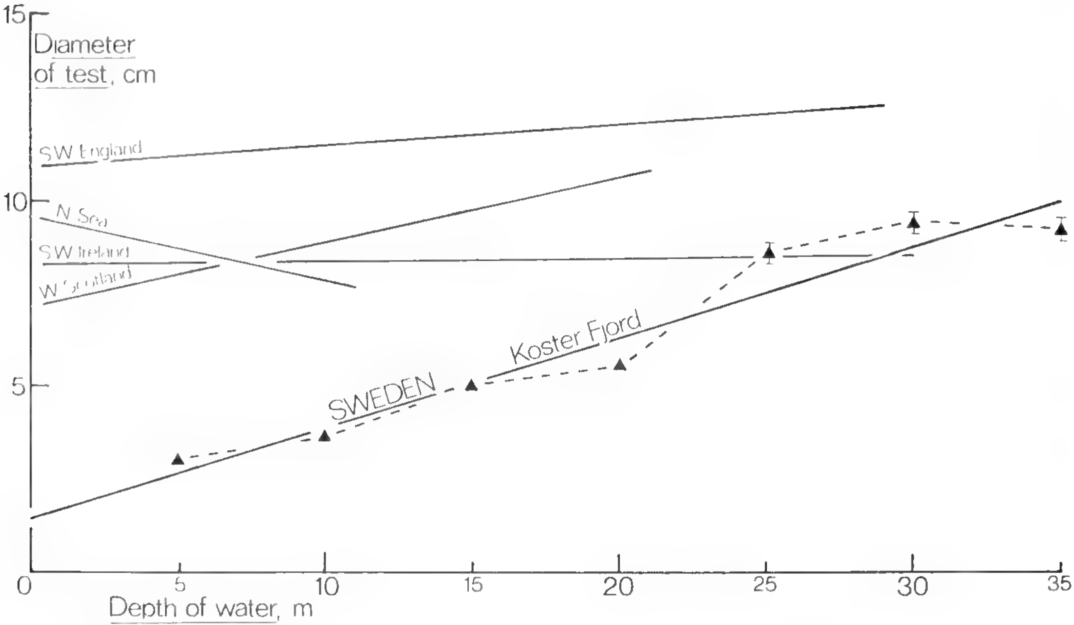


Fig. 7. Graph showing the relationship between mean values for test diameter and depth of water in which they occur (closed triangles) for the sea-urchin *Echinus esculentus* in the Koster Fjord, Sweden. Data extracted from Larsson (1968). Other conventions as in Figure 2. Regressions for the mean values for test diameters of urchins from the four British areas investigated in the present work are also included within the same axes for comparison.

Regression equations are as follows:

Koster Fjord.	$y = 1.433 + 0.242x$
South-West England.	$y = 10.88 + 0.035x$
North Sea.	$y = 9.49 - 0.168x$
South-West Ireland.	$y = 8.234 + 0.009x$
Western Scotland.	$y = 7.051 + 0.176x$

graph (fig. 5), reveals the following features: first, South-West England has populations of urchins that are significantly larger at all depths than elsewhere; secondly, in Western Scotland the size of urchins increases to a greater extent with increasing depth than in the other localities; thirdly, the North Sea urchins alone, so far as meaningful conclusions can be drawn from these results, decrease in size with increasing depth of water; and, fourthly, the populations in South-West England and South-West Ireland show little significant change in size with increasing depth. That these general conclusions are not merely a factor of the different depths to which the various diving teams surveyed is borne out by the similarity in appearance of the graph if the results are recalculated down to only 15 m depth of water (fig. 6). This depth was chosen principally because it is within that to which all the separate sites were surveyed, except those in the North Sea, and also because it roughly corresponds to the depth to which algae, a principal food of *Echinus*, penetrate.

Insufficient data are available on the physical conditions in the areas and sites surveyed to suggest reasons for the features that have emerged. However, the following suggestions are made: perhaps the slightly warmer waters in South-West England induce a larger overall size of urchins in that area; perhaps a difference in the availability of food in shallow waters helps explain the small size of urchins in the shallowest populations of Western Scotland; perhaps there is a more rapid fall-off in the density of algae with depth in the turbid water of the North Sea causing a reduction in mean size of urchins with increasing depth in that area. The study

underlines the need for detailed physical, faunistic and floristic information to be considered alongside the biometrical data when surveys like this are undertaken if the biological significance of the trends uncovered is to be suggested.

Without similar additional information from the Swedish waters surveyed by Larsson in 1966 (fig. 7), it is just as difficult to suggest reasons for the marked differences between populations there and from the British Isles. The average size of the Swedish urchins is small in shallow waters, but increases at a greater rate with depth of water than those from any of the British areas, coming to overlap the British size ranges in deeper waters. Although the time of year of Larsson's survey is not known, it is unlikely that this, or a possible difference in the time of spawning of the Swedish population, could account for the difference between the Swedish and British populations.

For all the shortcomings in interpretation of these results, owing to the lack of ecological data taken with the initial measurements, the survey conducted by separate groups of divers, many of them amateurs, during Underwater Conservation Year in the United Kingdom, took the study of the population structure of *Echinus esculentus* much further than had previously been possible. It has underlined that there are regional differences in the overall size of individuals, a fact that could be significant to the curio industry now based on the dried test of the animal, and to any proposed industry based on its roe; it has shown that the population structure apparently can be affected by the exposure of the area; and it has suggested that the effects of human predation can be detected by surveys of this sort. More than this, however, it has demonstrated that the collection of scientific data can be aided by the activities of amateur divers, suitably briefed, and hopefully the experience gained by such people in taking part in such a programme will help them encourage others to conserve species like *Echinus* that are now under threat.

ACKNOWLEDGEMENTS

The Author thanks the Projects Officer of UCY 77, Dr Charles Sheppard, and his successor, Dr Bob Earll, for their help in involving diving teams in this survey; he also thanks Dr D. Stradling and Mr C. J. Lawrence for advice on statistical techniques and Dr A. B. Smith for helpful suggestions on the manuscript; finally he thanks the many individual divers and their organisers for all their hard work in collecting the data on which this paper is based.

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10. CHANGES IN THE ECHINODERM FAUNA IN A POLLUTED AREA ON THE COAST OF BRAZIL

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SUMMARY

The purpose of this research was to compare the changes in echinoderm fauna in a region under increasing eutrophication.

A preliminary survey of the fauna was conducted by Tommasi in 1964; such results here served as a baseline for comparison with the data obtained during a more thorough investigation made from 1974 to 1976 by a team from the Institute of Oceanography.

The animals were identified to species and their distributions correlated to environmental parameters like type of sediment, water temperature, salinity, depth and dissolved oxygen, as well as parameters indicative of pollution, mostly nutrients and turbidity.

The results for 1974 to 1976 period indicate a lower diversity as well as the disappearance of a number of species when compared to the 1964 period.

INTRODUCTION

The echinoderm fauna of the coast of the State of São Paulo, Brazil, has been studied by Bernasconi (1956) and by Tommasi (1957, 1958, 1965 and 1966). In 1964 Tommasi studied the distribution of these animals as part of a more thorough investigation of the benthic assemblages of the Bay of Santos (24°00'S, 46°20'W), his results were published in 1967, at which time considerable concern had already been aroused by drastic changes which had occurred as the result of sewage, dredgings as well as the installation of smelters and other industrial plants.

As pointed out by Isaacs (1973) the discharge of sewage as well as of industrial effluents in estuarine regions can affect the communities of benthonic invertebrates in two ways: (a) a great influx of organic matter tends to have a deleterious effect on filter feeders, detritus feeders and also on their predators; (b) the change in consistency of sediments, the increase in the level of heavy metals and toxic organic compounds, the reduction in dissolved oxygen as well as the increase in sulphides as a result of the deposition and decomposition of organic matter, may inhibit larval attachment or may have toxic effects directly on already attached larvae or on adults which may be sensitive to such pollutants.

From 1964 onwards the Santos region has suffered a considerable increase in eutrophication levels as a result of its development as a summer resort, accommodating during the summer months more than one million people, as well as the increase of its docking facilities and installation of new industrial plants.

In 1974 a joint programme was established between the Institute of Oceanography of the University of São Paulo and the State Centre for Basic Monitoring of Environment (CETESB) in order to investigate the present status of the animal assemblages and environmental conditions in the region. As part of this programme, a study was carried out on the distribution of the echinoderm fauna, similar to that carried out by Tommasi (1967). As much as possible, the echinoderm distribution and abundance has been considered in relation to environmental parameters such as nutrient content, temperature, salinity, type of sediment, dissolved oxygen and depth.

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DESCRIPTION OF AREA STUDIED

The bay and the estuary of Santos (24°00'S, 46°20'W) on the coast of the State of São Paulo (fig. 1) receive a very heavy load of organic pollutants as a result of the outflow of sewage effluents of the city of Santos and nearby villages. Aside from the several kinds of detritus and substances originating from mangroves and nearby rivers, a number of industrial wastes, sewage and oil residues are introduced in the Santos region. The final picture in the estuary and bay area is one of high water turbidity, high level of suspended material and considerable eutrophication of marine environment.

The area under study can be divided into two distinct regions, namely one in the west side and one in the east side of the bay of Santos. The more saline water which comes from the south penetrates under the more diluted water which leaves the estuarine area and the bay. This high salinity wedge which penetrates the east side of the bay is more pronounced than the one on the west side where there is a much greater mixture of deep and surface water.

Previous studies (Emilson, 1955) have shown that the west side of the bay is under heavier influence of the tidal currents, while the east side is characterized by waters originating from the estuarine area. Such a pattern of water circulation produces two distinct areas, one on the west side where there is a predominance of waters from the continental platform and the other on the east side where waters are mostly of low salinity, originating from the estuary of Cubatao River.

Also such a pattern exerts influence on the types of sediments of the bay; on the west side predominate medium and fine sand, while on the east side, finer sediments (silt) are to be found.

The granulometric analysis carried out by Tommasi (1967) indicated a predominance of very fine sediments in several stations of the area under study. On the southern part of the bay as well as along the shores predominated sandy bottoms while on the eastern side some of the stations provided samples with a number of dead shells, coarse sediments and detritic material.

The sample obtained in the last years showed only the presence of sediments ranging from 0.063 to 0.250 mm in diameter, namely from clay and silt to fine sand; silt and clay were found mostly near the estuary, very fine sand on the east side and fine sand along the beaches and west side of the bay.

Prevailing winds are from the coast during spring and summer, southerly winds predominating during fall and winter (Oliveira-Santos, 1965). Annual precipitation in the area reaches values of 2000 mm or more; highest levels are measured from January to March and the lowest ones in July and August (Camargo, 1960).

Mean values for salinity increase from 29°/00 in December (rainy season) to July 34°/00 (dry season). The curves for salinity and temperature (fig. 2) show an inverse relationship.

Values for dissolved oxygen and salinity are extremely variable in the channel, and estuarine region; salinity values as low as 5.5°/00 have been found in surface waters on some occasions, while that at the bottom remains fairly constant (27 to 32°/00). Temperature fluctuates from values as low as 16.6°C in the winter to 29°C in the summer, mean values ranging 17 to 27°C.

METHODS

The bottom samples were obtained with a Van-Veen bottom grab, which sampled an area of 0.10 m² and had a capacity of 10-12 litres. Periodic collections were made every season during the period December 1974 to November 1976 in 31 stations ecompassing all the estuary and Bay of Santos (fig. 3) to a maximum depth of 15 metres.

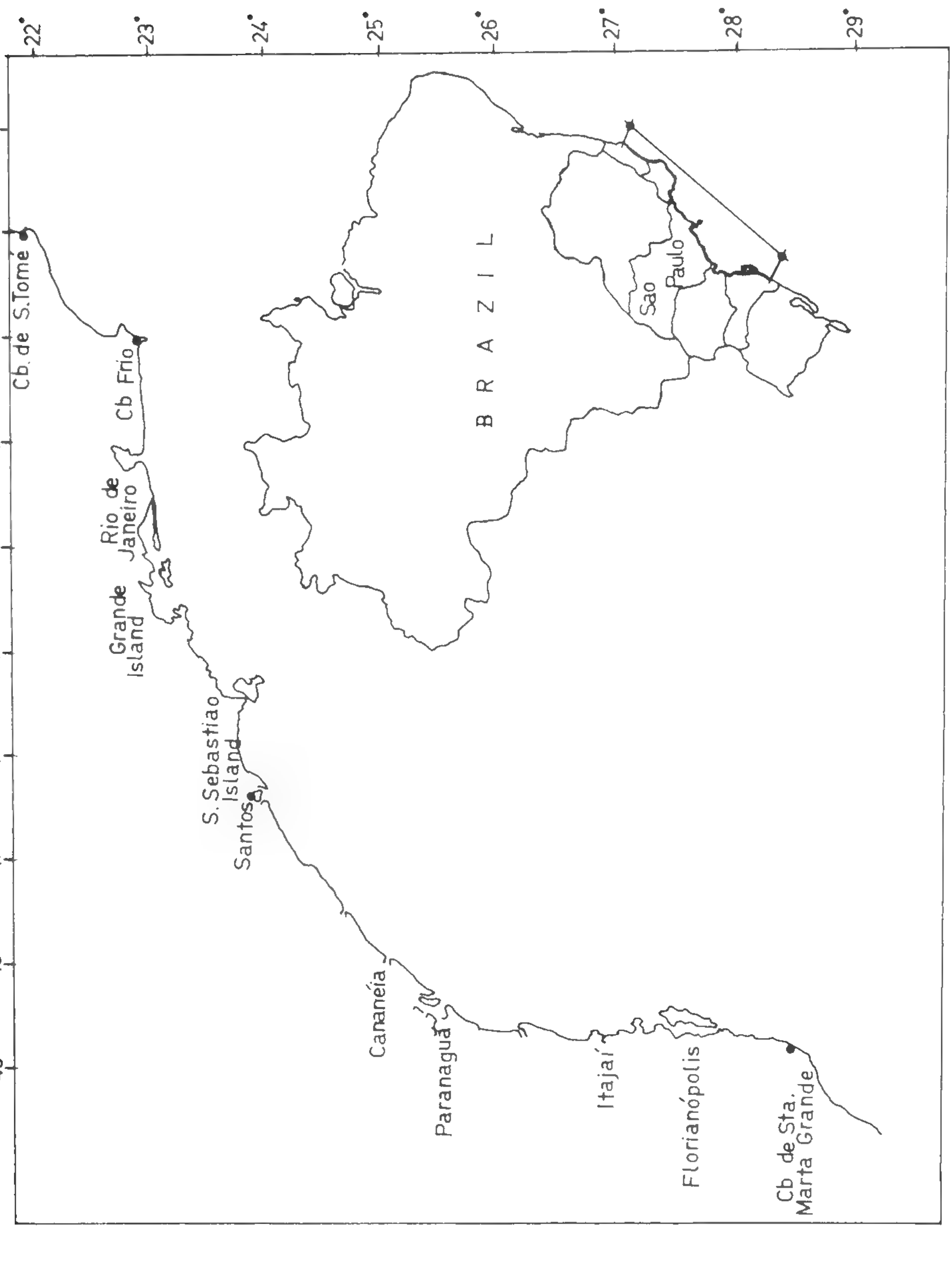


Fig. 1. City of Santos on the coast of Brazil.

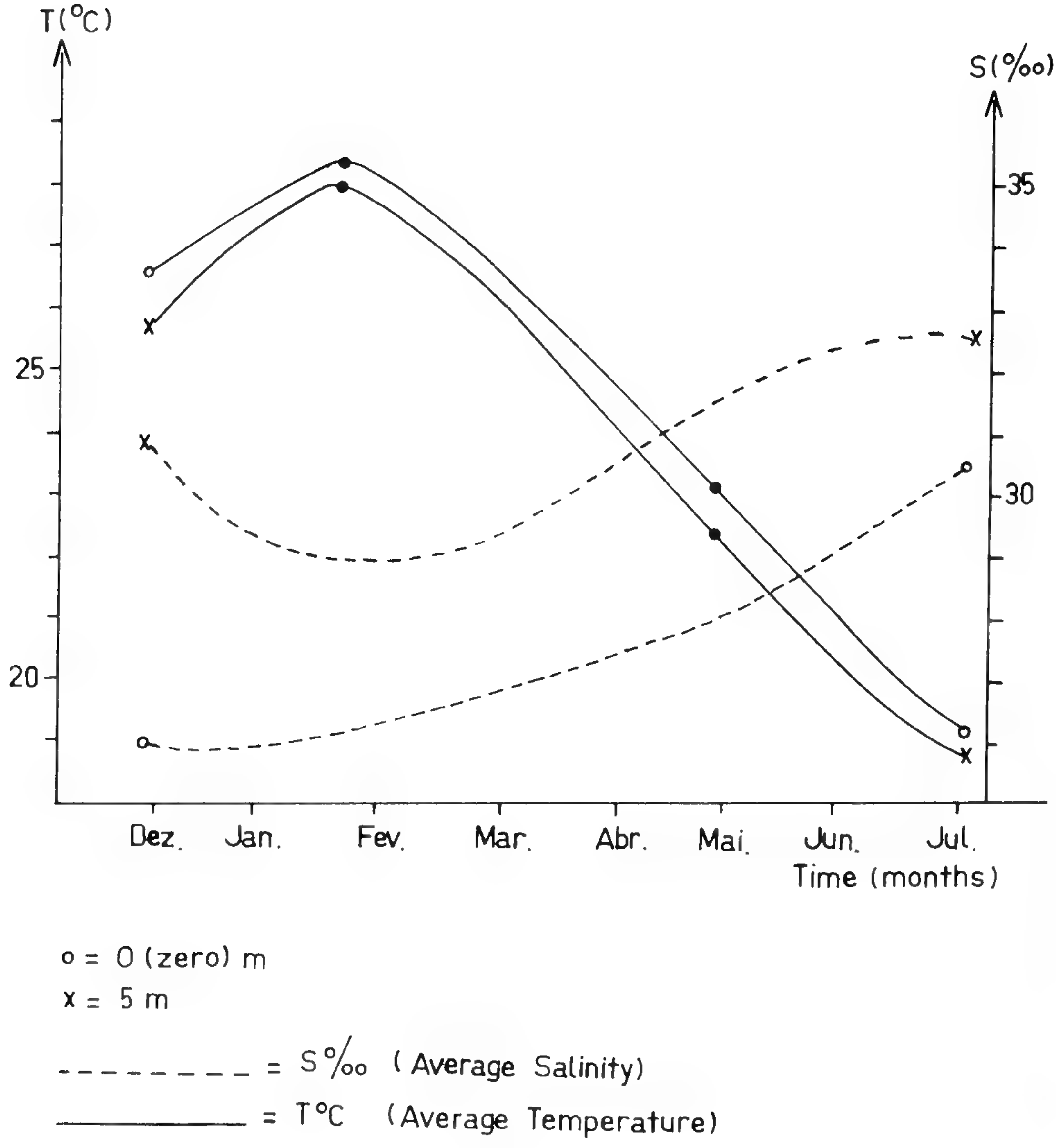
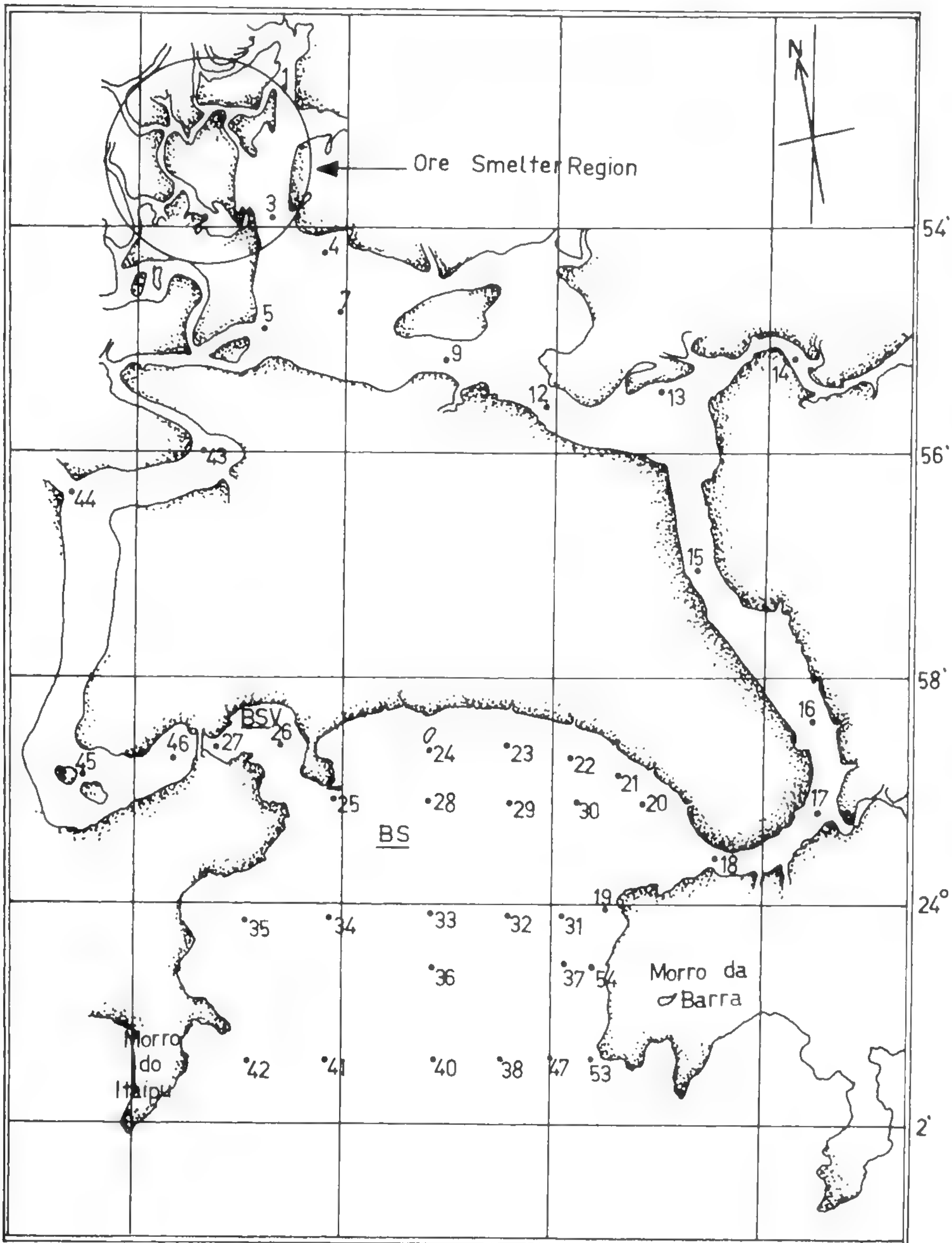


Fig. 2. Curves of salinity and temperature from the region studied.



BS = Bay of Santos

BSV = Bay of Sao Vicente

Fig. 3. Sampling positions in region studied.

In each station two bottom samples were obtained; on board the ship all the macrofauna was immediately separated by sieving the sample through 2 mm and 1 mm mesh. The animals were preserved for further examination under a stereoscopic microscope. The echinoderm specimens were then separated and identified down to species level.

Samples of water were also taken near the bottom for analysis of salinity, dissolved oxygen and nutrients (phosphate and nitrate); such analyses were conducted according to the methods recommended by Environmental Protection Agency (EPA) 1972 and Standard Methods for the Examination of Water (1971).

Also, a part of the bottom sample was separated to be used in the granulometric analysis.

RESULTS

Before presenting the results obtained in the present survey, it seems advisable to list those found by Tommasi in 1964. At that time 14 species of echinoderms were found, the ophiuroids being the most abundant group. The species included *Amphipholis januarii* Ljungman, *Hemipholis elongata* (Say), *Micropholis atra* (Stimpson), *Micropholis gracillima* (Stimpson), *Ophiactis lymani* Ljungman, *Ophioderma januarii* Lütken and *Ophiothrix angulata* (Say).

The asteroids were represented by *Astropecten brasiliensis* Müller and Troschel, *Astropecten marginatus* Müller and Troschel, *Echinaster brasiliensis* Müller and Troschel, *Coscinasterias tenuispina* (Lamarck) and *Luidia senegalensis* (Lamarck). The occurrence of both crinoids and echinoids was restricted to *Tropiometra carinata* (Lamarck) and *Mellita quinquiesperforata* (Leske) respectively.

In the more recent samples (1974 to 1976), the animals collected included the ophiuroids *A. januarii*, *H. elongata*, *M. atra*, *M. subtilis* (Ljungman), *O. lymani* and *Ophiophragmus lütkeni* (Ljungman), the asteroids *A. marginatus* and *L. senegalensis;* the only echinoid found was *M. quinquiesperforata*, which occurred in fairly dense populations. The quantitative aspects of the samples are presented in Table 1, which shows that the more abundant species were the ophiurans *H. elongata* and *M. atra*.

The crinoid species *T. carinata*, the asteroids *A. brasiliensis, E. brasiliensis, C. tenuispina*, and the ophiuroids *M. gracillima, O. januarii* and *O. angulata* were not found in any of the samples.

In the eastern position of the bay, next to the Morro da Barra, mostly in station 19 and 31, high densities of the ophiuroids *M. atra* and *H. elongata* were found. Tommasi (1967) had already pointed out that this region presented a much higher number of echinoderms as compared to other areas of the Bay. It is to be noticed that in station 19 and 31 the bottom deposits are constituted mostly of silt and fine sand.

In the region next to the beaches there was a predominance of sandy bottoms, the asteroid *A. marginatus* being the dominant species; on the west side of the bay the echinoid *M. quinquiesperforata* presented densities higher than any other species. Such a general pattern of distribution had already been observed in the 1964 samples.

During all the sampling period no echinoderms were found in the estuarine region; the only records are those for station 18, near the entrance to the channel.

The nutrient levels in station 1, fairly close to the iron smelter plant, were about 10 times

higher than those generally found in the Bay. In station 1, the levels for PO_4 and NO_3 were respectively 0.44 mg/l and 0.21 mg/l, dissolved oxygen being of order of 1.8 mg/l; transparency of water is reduced to about 0.85 m, the bottom being constituted mostly of silt and clay.

In station 16, typical for most of the channel, values for nutrients were around 0.17 mg/l for PO_4, 0.16 mg/l for NO_3 and 4.9 mg/l dissolved oxygen; transparency of the water was usually close to 1.75 m.

Station 19, which presented the greatest concentration of echinoderms, is located on the east side of the bay; levels for nutrients were of the order of 0.01 mg/l PO_4 and NO_3, 6.4 mg/l dissolved oxygen and transparency of the water around 1.10 m. The bottom is constituted mostly of very fine sand and silt, similarly to station 31.

In the western part of the Bay, the bottoms are mostly of fine sand; stations 26 and 27 presented fairly large population of *Mellita quinquiesperforata*. Measurements of PO_4 and NO_3 showed values of 0.07 mg/l and 0.15 mg/l respectively, dissolved oxygen being around 6.7 mg/l.

DISCUSSION

The analysis of the results obtained for the two different sampling periods shows a fairly definite change in the echinoderm fauna in the area under consideration, suggesting different tolerance limits for different echinoderm species in relation to the environmental parameters under consideration.

Due to the lack of information in relation to some of the environmental parameters (like nutrients) for the 1964 sampling, it is not possible to carry out a more detailed comparison with the more recent information.

It would seem that the disappearance of some of the species is to be correlated with change in the nature of the bottom sediments, due to continued dredging operations near the docking facilities in the channel and the removal of the new material to the vicinity of Itaipu Point. The construction of new roads in the same general area has also helped produce the present picture of a substrate consisting mostly of very fine material. The importance of the type of sediments in the distribution of benthic species has already been discussed by Beanland (1940), Holme (1949) and Sanders (1958).

As already mentioned, *Tropiometra carinata*, *Coscinasterias tenuispina*, *Echinaster brasiliensis* and *Ophiothrix angulata*, all characteristic of hard bottoms, were collected in 1964, but were not found again during the 1974-1976 period. They had been found associated with bottoms constituted of "detritic" material and dead shells, in areas which are now covered by sediments in the range 0.062 mm to 0.088 mm.

Special reference should be made to *Hemipholis elongata* and *Micropholis atra*, the two ophiuroid species which have predominated in soft bottoms on different occasions and which can occur in fairly high concentrations at some stations. The changing environmental conditions seem to have had little or no effect on the number and distribution of these two species.

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Table 1. Quantitative aspects of the samples. List of species, total specimens from each station, total specimens collected (n) and percentage of occurrence (%).

Sp. \ St.	18	19	20	21	22	23	24	25	26	27	29	31	32	33	34	35	37	40	41	42	47	54	n	%
Astropecten marginatus	—	—	—	—	2	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	3	0.46
Luidia senegalensis	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0.15
Mellita quinquiesperforata	—	—	9	1	—	—	—	3	19	—	—	—	—	—	—	5	—	—	1	71	—	—	109	16.72
Amphipholis januarii	—	6	2	2	—	—	4	—	—	—	—	—	—	14	—	—	—	11	—	—	—	—	39	5.98
Hemipholis elongata	4	1	1	—	12	1	—	4	2	—	6	144	61	63	19	10	6	66	—	12	1	—	413	63.34
Micropholis atra	3	35	1	2	6	—	1	—	6	1	2	—	—	3	—	1	—	—	—	—	—	16	77	11.81
Micropholis subtilis	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	6	0.92
Ophiactis lymani	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0.31
Ophiophragmus lutkeni	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	2	0.31

11. A STABLE SYSTEM OF PREDATION ON A HOLOTHURIAN BY FOUR ASTEROIDS AND THEIR TOP PREDATOR

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SUMMARY

Seven species of asteroids feed on *Cucumaria lubrica*, but together they harvest only 3% of the population or 10% of the standing crop biomass per year at the locality of the study. The rates of predation by the asteroid *Solaster dawsoni* on the predators of *C. lubrica* are high enough and the rates of growth and successful recruitment into the area by the predators of *C. lubrica* are low enough to indicate that the predators of *C. lubrica* are possibly kept low in abundance by the higher predator *Solaster dawsoni*. *Solaster stimpsoni*, the most abundant predator of *C. lubrica* in the area, has a behavioural escape mechanism which becomes increasingly effective as *S. stimpsoni* grows large and when it is on vertical rock surfaces. While *S. dawsoni* removes about 24-32% of the *S. stimpsoni* population each year, probably preventing a buildup in numbers, the refuge in size of a reproductive stock allows the persistence of the long-lived, slow-growing, *S. stimpsoni*. *Dermasterias*, a predator of *C. lubrica* with a refuge in size but with no behavioural escape mechanism to *S. dawsoni*, is 0.07 times as common as *S. stimpsoni* with a size-frequency distribution represented predominantly by large adults. *Solaster endeca* and *Leptasterias*, predators of *C. lubrica* with no known refuge to *S. dawsoni*, are 0.004 and 0.008 times as common as *S. stimpsoni* and may be considered strays from other habitats. No significant changes in abundance were observed in the 3 trophic levels of the association from 1965 to 1976: *C. lubrica*, 4.4×10^3 m^{-2}; *S. stimpsoni*, 0.5 m^{-2}; *S. dawsoni*, 0.007 m^{-2}. The stability of the system results from different control mechanisms and refuges at each trophic level.

INTRODUCTION

In basic ecological theory, predator-prey systems have an inherent tendency to oscillate or to become extinct (Lotka 1920; Volterra 1926; Gause 1934; May 1973). In natural systems, populations usually fluctuate to a much lesser degree than would be expected (Murdoch and Oaten 1975). The factors preventing over-exploitation of a prey by its predators fit into two general categories (MacArthur 1972:31): (1) a refuge for the prey or (2) a factor limiting the predators to numbers low enough to prevent annihilation of prey (e.g., a higher level predator, a limiting resource other than the prey in short supply, cannibalism, territoriality, etc.). Prey refuges stabilize a community by providing protection for a reproductive stock but allowing relatively easy access of the predator to the "surplus" (Errington 1946) or excess "product" (Connell 1970; Smith 1972) of the prey population. For the simpler organisms in a heterogeneous environment, the susceptibility of prey to predation is usually inversely related to their abundance. The prey with the weakest escape or defence responses or those in the least safe location are caught first; so as prey become more scarce, only the less available are present. Also, scarcity and unpredictability can become refuges in themselves, even if site selection is disregarded (Smith 1968; Birkeland 1974). The effects of refuges are generally inversely related to prey population size and are thereby a stabilizing factor in predator-prey systems.

As pointed out by Elton (1927), species size distribution has a major influence on community organization. The "size of the prey of carnivorous animals is limited in the upward

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direction by the carnivore's strength and ability to catch the prey, and in the downward direction by the feasibility of getting enough of the smaller food to satisfy the carnivore's needs" (Elton 1927:60). A number of predators, even those quite generalized in their diets, will take only earlier age classes from the prey populations. Prey individuals that survive long enough will gain a refuge in size (Paine 1965, 1976; Dayton 1971). Many benthic marine invertebrates are characterized by the type III survivorship curve implying "extremely heavy mortality beginning early in life, but the few individuals which survive to advanced ages have a relatively high expectation of further life" (Deevey 1947:286). A refuge in size is prevalent among marine invertebrates (Thorson 1955, 1958, 1961; Paine 1965, 1976; Dayton 1971; Connell 1972). However, in cases in which effective refuges do not exist, populations which sustain mortality in all age classes could be composed largely of the young stages (Grassle and Sanders 1973). An age structure composed preponderantly of long-lived adults also could imply a crowded habitat governed by competitive interactions (Pianka 1970) or unpredictable reproductive success (Murphy 1968). Therefore, similar age structures could be the manifestations of very different processes. To be used as evidence for the effects of a process, age structures must be presented along with natural history information and ample data on the rates of the critical process. In this paper we examine a predator-prey system which displays remarkable constancy despite intensive predation at two trophic levels. Our goal is to elucidate the factors promoting stability.

In the San Juan Islands of Washington State, the holothurian *Cucumaria lubrica* H. L. Clark attains great population densities (4 to 6 x 10^3 m^{-2}) over extensive areas of rock or cobble substrata in shallow water (about 8 to 20 m depth). Within these areas, this holothurian species is preyed upon by 7 species of asteroids (3 of which are congeners) and forms the major portion of the diet of 4 of these predators (Mauzey, Birkeland and Dayton 1968). These predators are consistently common as a group and we have observed no major fluctuations in either prey or predator abundance over a period of eleven years. With this apparently opulent food supply, one would expect that total predator density might increase until the predators begin to eliminate their prey in local areas or at least seriously reduce its abundance.

OBSERVATIONS

Cucumaria lubrica is a small (up to 0.5g dry weight) dendrochirote holothurian which is numerically predominant over large areas of nearshore subtidal rock or cobble substrata in the San Juan Islands. The population density from November 1968 through May 1969 at Eagle Point (cf. Fig. 1, a map, in Mauzey, Birkeland and Dayton 1968) was estimated as 4420 ± 400 (±) m^{-2} from counts in eight 0.01 m^2 and four 0.06 m^2 quadrats. In the four quadrats of May 1969, an average recruitment of 7.7 x 10^3 m^{-2} additional tiny *C. lubrica* was observed. *Cucumaria lubrica* is thus numerically prevalent and, in fact, occupies up to 43% of the primary substrata in such areas as Black Rock (Fig. 1; Mauzey, Birkeland and Dayton 1968) and much of the area along the west shore of San Juan Island (e.g., Eagle Point and Edward's Reef). In 1972 the mean abundance from all samples from Eagle Point was 4380 m^{-2}, not significantly different from the 1968-1969 samples. Our observations over an eleven year period (December 1965 through August 1976) indicated that this is a stable condition; *C. lubrica* continued to occupy a major portion of the substrata at Eagle Point and Edward's Reef throughout this period. Like most dendrochirote holothurians, *C. lubrica* is a passive suspension-feeder, and a position with adequate access to the water current is potentially a limiting factor.

The size distribution of *C. lubrica* from dry weights taken on 239 specimens collected in November 1968 and February 1969 is shown in Figure 1. The size distributions from these two collections did not differ significantly, so the data from the two collections were combined. Five normal curves were extracted from the size distribution in Figure 1 by using the method of Cassie (1954). Assuming the different normal curves represent year classes, the longevity of *C. lubrica* was estimated as 5 years. Estimates of size classes derived from the method are given in Table 1.

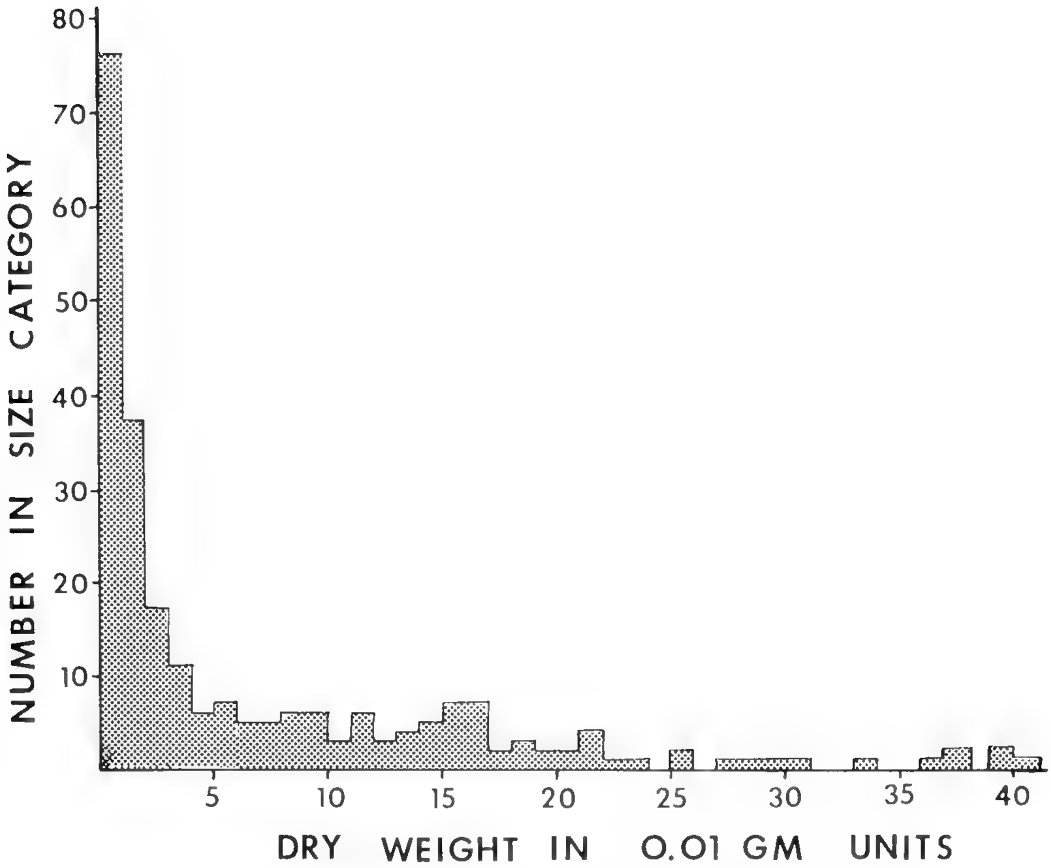

Fig. 1. Size distribution of *Cucumaria lubrica* at Eagle Point (at 10 m depth) from collections taken November 1968 and February 1969.

In areas in which it is predominant, this diminutive holothurian is preyed upon by seven species of asteroids (Mauzey, Birkeland and Dayton 1968): *Luidia foliolata* Grube, *Solaster stimpsoni* Verrill, *S. endeca* (Linnaeus), *S. dawsoni* Verrill, *Dermasterias imbricata* (Grube), *Leptasterias hexactis* (Stimpson) and *Pycnopodia helianthoides* (Brandt). While four of these species are generalists (*L. foliolata*, *D. imbricata*, *L. hexactis* and *P. helianthoides*) and prey upon organisms other than holothurians in areas where holothurians are not predominant, the abundances of the *Solaster* species appear to be related to the abundance of dendrochirote holothurians (Mauzey, Birkeland and Dayton 1968).

Luidia foliolata and *Pycnopodia helianthoides* only occasionally feed on *C. lubrica*. Forty-four percent of the observed prey items (N=61) of *L. foliolata* were holothurians and of these only about 47% (N=8) were *C. lubrica* (Mauzey, Birkeland and Dayton 1968). *Luidia foliolata* is characteristic of gently sloping or flat sand bottoms where it feeds on ophiuroids, holothurians and bivalves and is rare in current swept areas on solid substrata characterized by *C. lubrica*. Although large numbers of *C. lubrica* (17, 17 and 35) were found in *Pycnopodia* stomachs on 3 occasions, less than 2% of the feeding observations for *Pycnopodia* in the San Juan Islands included *C. lubrica* (Mauzey, Birkeland and Dayton 1968). Since *Luidia* and *Pycnopodia* only rarely eat *C. lubrica*, they will not be discussed further.

Table 1. Size class distributions of *Cucumaria lubrica* derived according to the methods of Cassie (1954).

Assumed Year Class	Dry Weight (10 mg units)		Standard Deviation	% of Total Collection*
	Mean	Range		
0	1.88	0.1 to 6.0	1.84	64.4
1	9.79	6.1 to 13.0	2.74	14.3
2	16.78	13.1 to 21.0	2.08	13.3
3	25.42	22.0 to 31.0	4.46	5.1
4+	38.30	34.0 to 41.0	4.49	2.9

*N = 239

Leptasterias hexactis and *Dermasterias imbricata* tend to specialize on *C. lubrica* in areas where *C. lubrica* is predominant, although they have very different diets in other areas. Small holothurians make up 82% of the diet of subtidal *L. hexactis* in the San Juan Islands (Mauzey, Birkeland and Dayton 1968), and *C. lubrica* comprises 85% of the holothurian prey or 69.7% of the total diet. In intertidal areas, however, *L. hexactis* feeds mainly on barnacles and molluscs (Menge 1972). In *C. lubrica* beds, 96.7% of the diet of *D. imbricata* ($N = 123$) is made up of dendrochirote holothurians and of these, 92.4% are *C. lubrica* (89.4% of the total diet). In other areas, however, over 95% of the diet of *D. imbricata* may be made up of anemones, sponges, or pennatulaceans (Mauzey, Birkeland and Dayton 1968; Birkeland 1974) or 45% echinoids (Rosenthal and Chess 1972). Twenty-three *D. imbricata* contained from 1 to 30+ *C. lubrica* in their stomachs, with a mean of 7.7 *C. lubrica* per stomach.

Solaster stimpsoni and *S. endeca* feed mainly on dendrochirote holothurians (Mauzey, Birkeland and Dayton 1968). In the San Juan Islands, we recorded 424 feeding observations for *S. stimpsoni* (64% of the 656 *S. stimpsoni* examined were feeding). Holothurians made up 96% (or 408) of the feeding observations and of these, *Cucumaria lubrica* accounted for 93% (89.3% of the total diet), *Eupentacta* sp. and *C. miniata* (Brandt) 2% each and *Psolus chitinoides* H. L. Clark 1%. The *S. stimpsoni* preying upon *C. lubrica* were found with 1 to 8 specimens of *C. lubrica* per seastar or with a mean of 1.6 + 0.9 s. *Solaster stimpsoni* spends 64% of its time feeding and 89% of its diet consists of *C. lubrica*. The average time required for digestion of a meal of *C. lubrica* was found to be 1.5 days for four observations in aquaria. Therefore, each *S. stimpsoni* eats about 222 *C. lubrica* per year. (This and similar calculations for the rate of predation on *C. lubrica* by the other species of asteroids are given in Table 2. The proportion of the *C. lubrica* population and biomass consumed by the combined activities of all asteroids is calculated in Table 3.)

One hundred thirty-eight *S. stimpsoni* were individually tagged with FD-67 Floy Tags. Within a year, most of the tagged seastars had disappeared, although many of these apparent disappearances could be simply a loss of tags with no sign of damage to the seastar. The *S. stimpsoni* recovered were individuals which had disappeared for several months, then reappeared. Other solasterids, *S. dawsoni* and *Crossaster papposus* (Linnaeus), are characteristically very motile (Mauzey, Birkeland and Dayton 1968; Birkeland 1974).

Although *Solaster stimpsoni* and *S. dawsoni* appeared to wander in and out of the area, they were relatively scarce in other areas and appeared not to be feeding as well in these other areas. We have examined many different habitats and localities between 1965 and 1976 (cf. also Mauzey, Birkeland and Dayton 1968). The percent of the *Solaster* that were feeding was lower in these other habitats (Birkeland 1974) and some of the prey items were of rather doubtful benefit to the *Solaster* (Mauzey, Birkeland and Dayton 1968; Birkeland 1974). For instance, *Solaster stimpsoni* feeds mainly on holothurians which were more scarce in these other habitats so the percent of the *S. stimpsoni* found feeding was lower. Sometimes *S. stimpsoni* was found with its rays wrapped around and its stomach extruded upon the surface of a sea pen, *Ptilosarcus gurneyi* (Gray), or over a tunicate, *Pyura haustor* (Stimpson). In these cases there was no sign of damage to the prey.

Although individual *S. stimpsoni* switched from "wall" to "wall" (areas in our study site) or disappeared while new individuals arrived in the area, the abundance of *S. stimpsoni* did not change significantly during the 9 year period (Table 4). The numbers of *S. stimpsoni* were counted on specific rock walls and on certain sections of horizontal cobble substrata in our study areas on 10 dates from 14 December 1967 to 13 August 1976. If we take dates as treatments or conditions and the six larger sample areas as subjects or replicates, we can use the nonparametric Friedman two-way anova by ranks (Siegel 1956) to test if the number of *S. stimpsoni* in the area varied significantly with time. Since the areas over which the counts were made must be complete matched sets for given dates, we tested the counts from the upper four rows (areas) in

Table 2. Rate of removal of *Cucumaria lubrica* by predation from six species of asteroids.

Predator Species	% of individuals found feeding (A)	% of diet consisting of *C. lubrica* (B)	Average No. of *C. lubrica* per stomach containing *C. lubrica* (C)	*C. lubrica* eaten per individual per year $\frac{(365\ ABC)}{1.5}$*	*C. lubrica* eaten per 100 m² per year**
Solaster stimpsoni	64	89	1.6	222	10955
Solaster endeca	62	58	1.0	88	18
Solaster dawsoni	53	7	2.0	18	13
Dermasterias imbricata	64	89	7.7	1067	3522
Leptasterias hexactis	44	70	1.0	75	30
Pycnopodia helianthoides	51	1	26.0	32	97
				TOTAL	14635

*A consumption and digestion time for *C. lubrica* of 1.5 days is assumed for each species of asteroid based on the average of four observations in the laboratory for *S. stimpsoni* and five observations in the laboratory for *Dermasterias*.

**Calculated from data in Table 5.

Table 3. A calculated estimate of the proportion of *Cucumaria lubrica* biomass consumed by all six species of its asteroid predators.

Age Class	a no. m^{-2}	b no. eaten m^{-2}	c g m^{-2}	d g eaten m^{-2}
SET	2835	—	53.3	—
1 (yearlings)	626	36.6	61.3	3.6
2	589	36.6	98.8	6.1
3	221	36.6	56.2	9.3
4+	129	36.6	49.4	14.0
TOTAL	4400	146.4	319	33.0

a. No. m^{-2} determined by apportioning the abundance of 4400/m^{-2} according to the ratio of the numbers in year classes from Table 1.

b. No. eaten m^{-2} acquired by evenly dividing the total from Table 2 among the larger year classes because *S. stimsoni* prefers larger *C. lubrica*.

c. G/m² derived by multiplying column a times the mean dry weight of each year class from Table 1.

d. G eaten/m² estimated by $\frac{\text{no eaten } m^{-2}}{} \cdot$ g m^{-2}

Table 4 for all dates except December 1967 and January 1969 for which counts were lacking in one of the areas. Although there appears to be an increase in the numbers of *Solaster stimpsoni* over the nine year period (Table 4), the Friedman two-way anova by ranks test indicates that there was a seventy to eighty percent probability that the differences could have been greater by chance. On five dates, counts were made in all six areas. We compared October 1967, November 1968, February 1969, January 1972 and August 1976 for all six areas and found that there was a ten to twenty percent probability that the differences between dates would have been greater by chance alone. Therefore, the *S. stimpsoni* population seems to be characterized by a stability in numbers during a constant wandering of individuals in and out of a given local area. This is characteristic of several seastar populations (Menge 1974), including *S. dawsoni* (Birkeland 1974). The mean abundances of *S. stimpsoni* and the seastars relevant to our discussion are given in Table 5.

Seven tagged *S. stimpsoni* were recovered after one year, three of these after 2.6 years, but no predictable growth patterns could be observed. After reaching a diameter of about 25 cm, *S. stimpsoni* may increase or decrease in size. Those seastars which decrease in total diameter (tip of ray 1 to tip of ray 6) look "unhealthy"; the rays are particularly thin and occasionally even have concave grooves. From these few data (Table 6) we estimated the growth of adult *S. stimpsoni* (excluding from the analysis those decreasing in size) at 2 cm total diameter per year. Presumably, small individuals would grow at a greater rate.

About 21% of the *S. stimpsoni* at Eagle Point during 1968 and 1969 ($N=74$) were infected with a parasitic green alga *Diogenes* sp. Two of the six tagged *S. stimpsoni* that decreased in size were heavily infected; none of the six that grew were infected. Both of the *S. stimpsoni* had been infected by *Diogenes* sp. during the entire observation period, so *S. stimpsoni* is able to survive with *Diogenes* sp. for at least 32 months. One untagged *S. stimpsoni* was observed to be very green and very near death, motionless with concave grooves in its thin rays.

Of a total of 42 field observations on *Solaster endeca*, 27 were feeding: 16 on *Cucumaria lubrica*, 3 on *C. miniata*, 2 on *Psolus chitinoides*, and 6 on bryozoa, tunicates and unidentified organisms. *Solaster endeca* was very rare in our study areas with 0.004 times the abundance of *S. stimpsoni* (Table 5).

Of 138 field observations on *Solaster dawsoni*, 65 (47.1%) were feeding: 39 (60% of those feeding) were feeding on *S. stimpsoni*, 5 on *C. lubrica*, 4 on *Crossaster*, 3 on *Dermasterias*, 3 on *Leptasterias*, 3 on *Mediaster*, 3 on arms autotomized from *Evasterias*, 2 on arms autotomized from *Pycnopodia*, and 1 each on *Henricia*, *Balanus crenatus* Brugiere and *Solaster dawsoni*. *Solaster dawsoni* is cannibalistic and will defend itself against predation by others of its own species with a response similar to that used by *S. stimpsoni* (cf. Fig. 2 in Mauzey, Birkeland and Dayton 1968).

The recorded diameter ratios of prey *S. stimpsoni* to predator *S. dawsoni* which had successfully captured them were 0.38, 0.72, 0.90, 0.94, 1.00, 1.00, 1.02, 1.03, 1.08, 1.09, 1.10 and 1.14; the prey-predator diameter ratios recorded for attacks in which *S. stimpsoni* ultimately escaped were 1.18, 2.18, 2.23 and 2.23. The probability of the 4 escapes of *S. stimpsoni* being only by those greater than 1.15 times the diameter of their predator while the 12 successful captures of *S. stimpsoni* were only by those less than 1.15 times the diameter of their predator was due only by chance would be $P=0.0011$ by a two-tailed Fisher exact probability test (Siegel 1956). From this we conclude that the defence response of *S. stimpsoni* is effective only in combination with a refuge in size of approximately 1.15 times the diameter of the *S. dawsoni* attacking it.

Since *S. stimpsoni* and *Dermasterias* have refuges in relative size, the number of asteroids available as prey to *S. dawsoni* increases as *S. dawsoni* grows larger. The *S. dawsoni* feeding on *C.*

Table 4. Counts of *Solaster stimpsoni* present on specific topographic areas at the Eagle Point study site during a 9 year period. The hyphens mean that no counts were made on the area on the given date.

SITE NAME	AREA (m^2)	14 X 67	11 XII 67	15 IX 68	10 XI 68	16 I 69	22 II 69	10 V - 2 VI 69	5 I 72	6 VII 74	13 VIII 76
WALL No. 1	40	26	22	12	15	19	14	22	30	24	40
WALL No. 2	40	10	13	12	10	7	9	9	15	16	27
FLOOR	32	8	—	12	14	8	7	9	8	26	32
OFFSHORE ROCKS	16	10	3	12	9	—	12	16	7	3	1
WALL No. 3	35	16	26	—	8	—	13	—	23	—	50
WALL No. 4	28	9	—	—	14	—	4	—	4	—	12
MEAN No./m^2		.41	.49	.38	.37	.30	.31	.44	.46	.54	.85

Table 5. Mean population densities at Eagle Point of the seastars involved in this study.

Topography	Total area sampled (in m^2)	Mean densities (No./100 m^2)					
		S. dawsoni	*S. stimpsoni*	*S. endeca*	*Dermasterias*	*Leptasterias*	*Pycnopodia*
Rock wall (vertical)	985	0.2	52.0	0.1	3.6	0.2	2.3
Cobble floor (horizontal)	1102	1.1	47.0	0.4	3.1	0.6	3.6
Total	2087	0.7	49.4	0.2	3.3	0.4	3.0

Table 6. Growth of tagged asteroids at Eagle Point.

Diameter in mm (tip of ray 1 to tip of ray 6) beginning	end	Time interval (months)	Growth rate (mm/mo.)
		Solaster stimpsoni	
218	252	14.1	2.41
257	287	14.1	2.13
277	270	6.6	-1.06
279	328	15.3	3.20
290	314	32.4	0.74
304	263	9.9	-4.14
304	312	9.9	0.81
315	302	6.6	-1.97
320	308	13.5	-0.89
325	339	10.4	1.35
328	320	31.8	-0.25
340	294	32.6	-1.41
Mean and standard deviation of growth rates		Only positive data included	1.77 ± .97
		All data included	.08 ± 2.10
		Dermasterias imbricata	
163	191	7.4	3.78
353	366	37.9	0.34
388	350	39.7	-0.96
Mean and standard deviation of growth rates		Only positive data included	2.1 ± 2.4
		All data included	1.1 ± 2.4

lubrica for which we have measurements were 9.2, 12.5 and 16.7 cm in diameter. Since only small *S. dawsoni* have been found feeding on *C. lubrica*, we interpret this to mean that *C. lubrica* probably serves as only an alternative food for small *S. dawsoni* which would prey upon asteroids if they could capture them. Indeed, a *S. dawsoni* 4.8 cm in total diameter was found consuming a 4.9 cm *S. stimpsoni*. When *S. dawsoni* is in areas where dendrochirote holothurians and asteroids of accessible size are rare, it will resort to cannibalism (Birkeland 1974). Food availability and cannibalism are the only factors we have found so far that might set an upper limit to the abundance of *S. dawsoni*, a top predator.

The time necessary for capture and consumption of asteroid prey by *S. dawsoni* was measured in the field and the average time required was found to be 4.5 days (Birkeland 1974). However, when the prey to predator diameter ratio for *Crossaster*, which uses the typical solasterid defense response, increases to about 0.7, *S. dawsoni* requires 6 days to complete the attack and consumption. In our single accurately timed field observation of *S. dawsoni* preying upon *S. stimpsoni*, 6 days were required for a 23.8 cm *S. dawsoni* to capture and consume a 16.5 cm *S. stimpsoni*. Six days could be a general underestimate of the time required because the above prey to predator diameter ratio (0.7) is fairly low for a successful attack.

Assuming that *S. dawsoni* requires about 6 days to capture and consume a *S. stimpsoni* and assuming 47% of the *S. dawsoni* are feeding, then *S. dawsoni* spends an average of approximately 7 days between meals or eats 1 meal every 13 days or 28 meals per year. Since 60% of the diet of *S. dawsoni* consists of *S. stimpsoni*, each *S. dawsoni* eats about 17 *S. stimpsoni* per year. There are 0.7

S. dawsoni per 100 m^2 (Table 5), so *S. dawsoni* predation removes about 12 *S. stimpsoni* per 100 m^2, or about 24% of the standing crop of *S. stimpsoni* per year.

There may be a bias in our calculations towards an overestimate of the number of *S. stimpsoni* consumed by *S. dawsoni* because the measured times required for consumption were obtained from situations in which the prey: predator diameter ratios were low. However, there may also be a conservative bias in our calculations towards fewer *S. stimpsoni* eaten per year because we may tend to find larger *S. stimpsoni* as the prey of *S. dawsoni*. Smaller *S. stimpsoni* take less time to digest and we have less chance of recording them. If we assumed *S. dawsoni* takes 4.5 days to capture and consume a meal (the average time recorded in all our field observations) then by the same calculations as above, *S. dawsoni* predation would remove approximately 32% of the standing crop of *S. stimpsoni* per year. Similar calculations for *S. dawsoni* estimate that 44 to 59% of its standing crop is possibly removed by cannibalism each year.

DISCUSSION

Theoretical reviews of predator prey systems usually discuss systems with either one predator-one prey or one predator-several alternative prey species interactions (e.g., Murdoch and Oaten 1975). A common system is structured with several predator species obtaining the majority of their food from a single prey species (Elton 1927; Feeney 1970; Birkeland 1974). The prevalence of this several predators-one prey system is often referred to in the general ecological literature (Elton 1927; Smith 1972; Birkeland 1974) but avoided in theoretical reviews of predator-prey interactions.

In order for several of the predators to specialize on a single prey species, the system must be stable enough to provide a dependable food supply to the predators. We have investigated this asteroid-*Cucumaria lubrica* system in an attempt to discover the possible mechanisms that prevent the expected over-exploitation of this single resource under the combined pressure from a variety of predators and which provide the stability to the system.

The asteroid-*Cucumaria lubrica* system is not closed and the individual seastars will wander in and out of the area although the species are always present as a group. Some of these species probably obtain a significant proportion of their diet from other areas and from prey species other than *C. lubrica* in these other areas. But this doesn't answer the question of how *C. lubrica* can remain so abundant under the constant predation pressure of this variety of predators. The alternative prey in other habitats could tend to increase the effectiveness of the predators in keeping the population of *C. lubrica* at lower levels of abundance (Flaherty 1969), at levels too low to support those predators such as *S. stimpsoni* that specialize on them. *Solaster stimpsoni* is relatively scarce in other habitats where they don't feed as frequently and their alternative prey are sometimes of dubious value to them.

As is often the case in temperate marine communities, the diets of these predators diverge when they are found in different habitats but converge on a single resource when they are found together for long periods of time (Birkeland 1974). The resource, *Cucumaria lubrica*, is an example of what Elton (1927: 57) termed a "key-industry" species and the several predators that rely heavily upon it make up a "guild" in the sense of Root (1967). *Cucumaria lubrica* does not have any behavioural, structural or chemical defence or escape mechanisms. Unlike the other dendrochirote holothurians in the area, it does not often live in crevices or partially under rocks, but lives in abundances of four to six thousand per square metre out on open flat exposed rock or cobble surfaces. Food resources that are abundant, palatable and easily accessible to predation are often thought to have a refuge in "unpredictability" (cf. Coe 1956; Smith 1968; Janzen 1970, 1971; Birkeland 1974). This would not seem to apply to *Cucumaria lubrica* because *C. lubrica*

broods its offspring (Atwood and Chia 1974). Recruitment from an abundant brooder presumably occurs usually within an area in which the adults already occur. The abundances of thousands per square metre were maintained with remarkably little fluctuation in the same areas through our eleven years of observation.

The combined predation pressure from all the asteroid species is estimated by the calculations in Table 2 as removing 146 *C. lubrica* per m^2 per year. The mean abundance of *C. lubrica* was 4420 m^{-2} in 1968-1969 and 4380 m^{-2} in 1972. Predation by asteroids accounts for only about 3% of *C. lubrica* mortality or removal of only about 10% o the total standing crop in gms (Table 3). Thus it appears that asteroids which feed on *C. lubrica* have a consistently available food supply. It is most likely that some factor other than food availability must be restricting the increase in abundance of the predators of *C. lubrica*.

Our calculations for the rate of predation by *S. dawsoni* indicates that 24 to 32% of the standing crop of *S. stimpsoni* could possibly be removed during a year. The portion of the size distribution of *S. stimpsoni* greater than 18 cm resembles a single normal curve (fig. 2). If we assume that this represents the "reproductive stock" population while the smaller individuals represent "recruitment", then recruitment replaces less than 15% of the standing crop. The slow growth rate of seastars suggests that this "recruitment" may represent the recruitment of several years. If this is so, then our estimate of the impact of *S. dawsoni* predation on *S. stimpsoni* is an underestimate. Our calculations imply that *S. dawsoni* should be causing the local extinction of *S. stimpsoni*. This is clearly not occurring (Table 4). *Solaster stimpsoni* is over 70 times as abundant as *S. dawsoni* (Table 5) and remains consistently common (Table 4). Therefore some of the prey may not be available to *S. dawsoni*.

The size distribution of *S. stimpsoni* is predominated by the larger individuals (fig. 2) despite the very slow growth rate of adults (Table 6). Although the young *S. stimpsoni* are generally available as food for *S. dawsoni*, the defense response of *S. stimpsoni* evidently provides a refuge from *S. dawsoni* with a diameter less than 87% of its own. Further, *S. stimpsoni* has a refuge from *S. dawsoni* in space as well as size. It can be seen from the data in Table 5 that about 5 times as many *S. dawsoni* are found foraging on horizontal surfaces compared with vertical surfaces. When *S. dawsoni* commences an attack on *S. stimpsoni* and the latter begins its defense response, the leading rays of both individuals are lifted from the substratum. We have not actually observed an attempted attack by *S. dawsoni* on a large *S. stimpsoni* taking place on a vertical surface. However, if *S. dawsoni* ever made such an attempt, the outcome would likely be that both predator and prey would tumble from the wall. If they were separated during the fall, the *S. dawsoni* would probably lose the *S. stimpsoni* since it locates prey by chance physical contact (Feder and Christenson 1966; Mauzey, Birkeland and Dayton 1968). Small seastars (*Leptasterias* and small juveniles of other species) are susceptible to *S. dawsoni* predation on vertical surfaces since capture and consumption of them does not require *S. dawsoni* to release its hold on the substratum. Most instances of *S. dawsoni* feeding on *C. lubrica* were observed on vertical surfaces.

The rate of mortality of *S. stimpsoni* due to infection by *Diogenes* sp. is insignificant in comparison with the rate of mortality due to predation by *S. dawsoni*. We have observed that a *S. stimpsoni* can survive at least 32 months while heavily infected with *Diogenes*. However, the alga eventually dissolves the skeletal ossicles and will kill the seastar. The *Solaster* infected with *Diogenes* that were observed over a two year period all decreased in size (N=3). Infection by *Diogenes* will eventually kill those *S. stimpsoni* that have attained an essentially complete refuge in size from predators (fig. 2), thereby preventing a buildup in numbers in the size refuge, although this process may take a very long time. Infection by *Diogenes* could also increase the probability of mortality through predation by weakening the escape response.

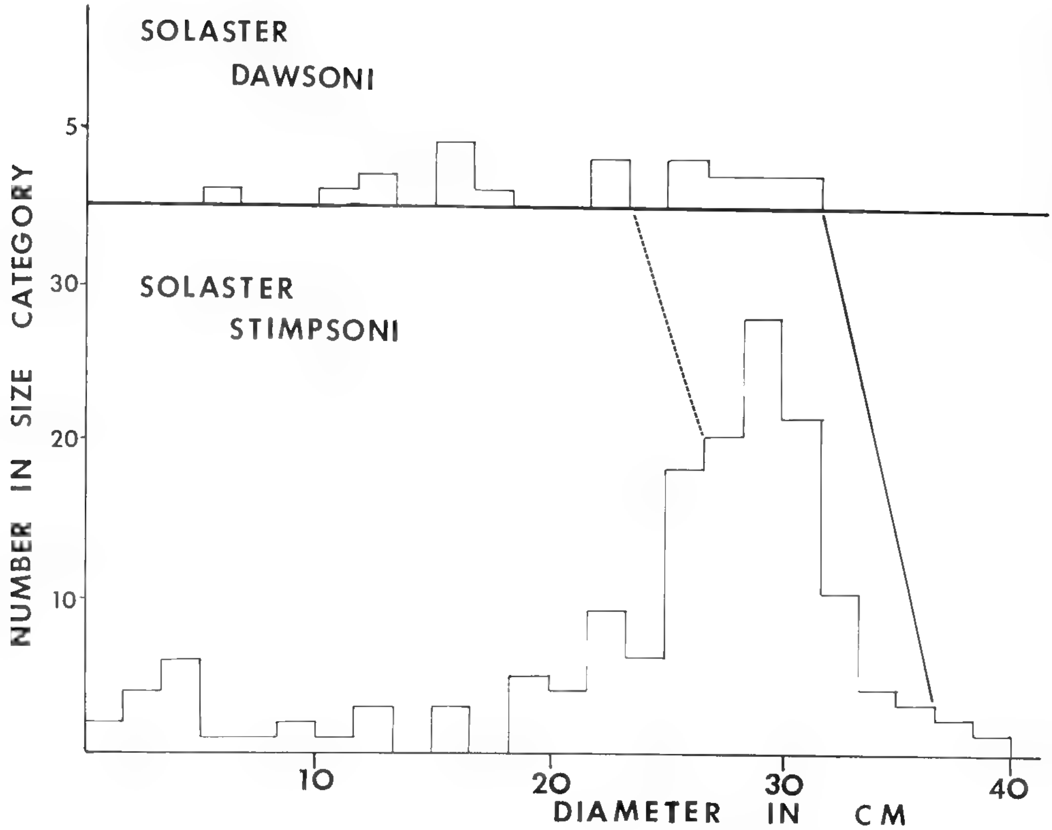

Fig. 2. Size distributions of *Solaster dawsoni* and *Solaster stimpsoni* at Eagle Point. Those *Solaster stimpsoni* larger than the size at the intersection with the broken line are safe from 50% of the *S. dawsoni* population by a refuge in size. Those to the right of the solid line have attained an essentially complete refuge in size from predation.

In contrast to *S. stimpsoni*, *S. endeca* does not have a defence response to predation by *S. dawsoni* (cf. fig. 2 in Mauzey, Birkeland and Dayton 1968 and fig. 3 in this paper). Probably due to this in part, *S. endeca* is the rarest member of the association (Table 5); *S. stimpsoni* is about 250 times as abundant. Similarly, *Leptasterias* is too small to escape *S. dawsoni* once attacked, although its small size may allow it to forage into crevices or cavities under cobble that *S. dawsoni* would pass over. The *Leptasterias* in the subtidal *C. lubrica* meadows have probably strayed from the intertidal part of their range where *S. dawsoni* very rarely wanders. *Dermasterias* has no behavioural defence or escape mechanism, but it can eventually grow too large to be consumed by *S. dawsoni*. With the lack of a behavioural mechanism that increases the effectiveness of the refuge in predator-prey size ratio, *Dermasterias* is only about 7% as abundant as *S. stimpsoni*. Once attaining the refuge in size, *Dermasterias* is susceptible to eventual mortality from infection by *Diogenes*. When attacked by *S. dawsoni*, *Pycnopodia* will autotomize one of its rays, which the *S. dawsoni* eats as *Pycnopodia* leaves the area.

The most remarkable aspect of this food-web association is its relative constancy in abundance from year to year at all trophic levels. The *C. lubrica* population maintained an abundance of 4.4×10^3 m^{-2} from 1968 to 1972. Our observations indicated no major differences

Fig. 3. *Solaster dawsoni* preying upon a *Solaster endeca* with a *Solaster stimpsoni* about 20 cm away. Note the lack of a behavioural escape or defence response by *S. endeca*. The dark tufts are tentacles of *C. lubrica*. *Cucumaria lubria* covers a major portion of the substratum.

from 1965 to 1974. Its most common predator species, *Solaster stimpsoni*, did not significantly differ in abundance through a nine year period (Table 4). The top predator, *S. dawsoni*, averaged 0.7/100 m^2 (2087 m^2 sampled) in 1968-1969 and 0.7/100 m^2 (648 m^2 sampled) in 1972. The interactions controlling the populations of these species differ with trophic level. A large portion of the individuals or available biomass of the *C. lubrica* population is left by predators (Table 3).

The prevention of overexploitation of *C. lubrica* might be explained as follows: *Solaster endeca*, *Leptasterias*, *Dermasterias* and *Pycnopodia* are all rare in the areas of *C. lubrica* under study because of predation by *S. dawsoni*. *Solaster endeca* and *Leptasterias* do not maintain a reproductive stock in the area. The few individuals present had strayed in from outside areas or wandered down from the intertidal and were temporarily missed by *S. dawsoni*. *Pycnopodia* is rarely killed by *S. dawsoni*, but leaves the area (often losing a ray) when attacked. *Dermasterias* does maintain a reproductive stock in the area, but recruitment to this stock may be limited by *S. dawsoni*.

Recruitment to the *S. stimpsoni* population is seriously impaired by predation, but the

reproductive stock remains consistently common because of a behavioural defence mechanism that becomes increasingly effective with size and works especially effectively on vertical substrata that serve as spatial refuges.

Predation by *Solaster dawsoni* keeps *S. endeca, Leptasterias* and *Pycnopodia* from establishing populations in meadows of *C. lubrica*. *Solaster stimpsoni* and *Dermasterias* can maintain a reproductive stock in the area with a refuge in size, but with severe predation on the recruitment to these populations, *S. dawsoni* can prevent *S. stimpsoni* and *Dermasterias* from increasing to population sizes capable of overexploiting their food resource. The slow buildup of populations of seastars having reached this size refuge is most likely prevented by infection from the parasitic green alga *Diogenes* sp. These processes together contribute to the maintenance of a remarkable constancy in numbers of this association at three trophic levels.

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12. THE SHRIMPS ASSOCIATED WITH INDO-WEST PACIFIC ECHINODERMS, WITH THE DESCRIPTION OF A NEW SPECIES IN THE GENUS *PERICLIMENES* COSTA, 1844 (CRUSTACEA: PONTONIINAE).

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SUMMARY

At present, fifty one species of shrimp are known to live in association with Indo-West Pacific echinoderms. Of these, only one is a stenopodidean, all others belong to the Caridea, principally to the subfamily Pontoniinae (35 species), with the others in the families Alpheidae (11 species) and the Gnathophyllidae (4 species). The echinoderm hosts may belong to any class but are mainly the Crinoidea (26 species), Echinoidea (18 species) and Asteroidea (18 species), although only a very small number of shrimp species are associated with the latter class. Three ophiuroids, all basket stars, and eight species of holothurians are known to have shrimp associates. The available knowledge of the biology of these associations is outlined.

Keys for the *provisional* identification of these shrimps are provided and one new species, *Periclimenes ruber*, is described and illustrated. The distribution of the shrimps is outlined and the known hosts listed.

INTRODUCTION

The shrimp fauna of the tropical and subtropical Indo-West Pacific region is dominated, in shallow water, by three groups, the Pontoniinae, the Alpheidae and the Hippolytidae. Numerous species of these groups are now known to live in "commensal" association with other marine animals. The details of these associations are very poorly known, and the use of the term "commensal" is, in general, rather misleading as it implies that something is known about the trophic relationships involved. This is rarely the case, and in the vast majority of examples virtually nothing is known about the feeding methods concerned. The use of the term "associates" is probably preferable in the present state of ignorance, especially as it seems probable that a variety of feeding strategies may be involved.

Associations between shrimps and other marine animals are particularly common in the warm tropical waters around coral reefs and are relatively infrequent in colder waters. Only a single example is known from the British Isles, *Typton spongicola* Costa, a pontoniine shrimp that lives in sponges. Little is known of these associations in deep water but they appear to be less frequent. Species of many shrimp families do occur in depths well over 100 fms and some of these probably are "commensals".

SYSTEMATIC ACCOUNT

Keys are provided below for the provisional identification of the known shrimp associates of Indo-West Pacific echinoderms. Where possible these identifications should be based on ovigerous females, and should be checked in detail with the original or later descriptions for confirmation. The keys will not separate related species found on non-echinoderm hosts.

KEY TO THE GENERA OF SHRIMP ASSOCIATED WITH INDO-WEST PACIFIC ECHINODERMS

1. First two pairs of pereiopods with chelae 2

—. First three pairs of pereiopods chelate .... *Odontozona*

*Present address: The Darwin Museum, P.O. Box 1646, Darwin, N.T., Australia 5794.

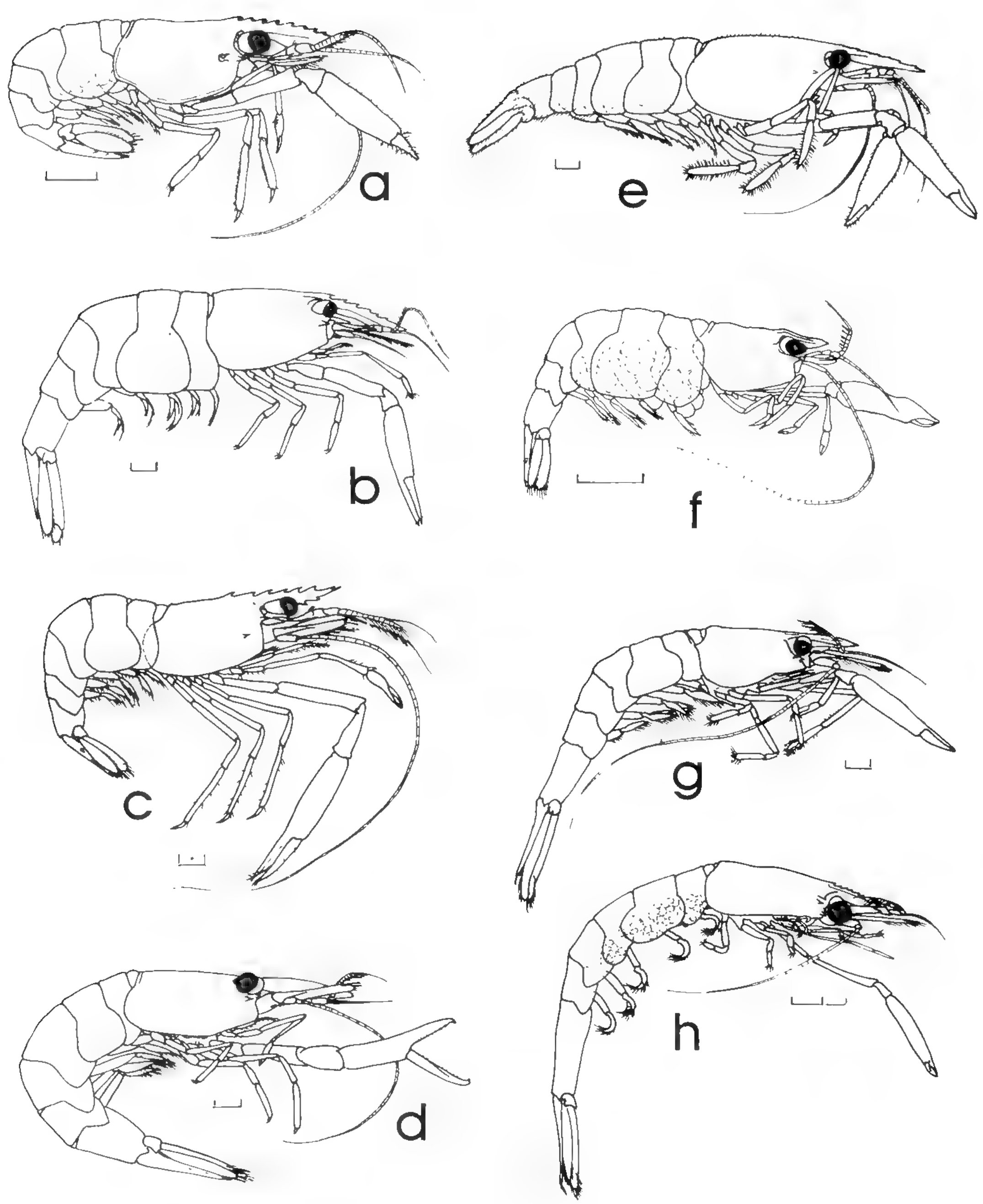

Fig. 1. **a.** *Allopontonia iaini* Bruce, **b.** *Araiopontonia odontorhyncha* Fujino & Miyake, **c.** *Palaemonella pottsi* (Borradaile), **d.** *Parapontonia nudirostris* Bruce, **e.** *Periclimenes hirsutus* Bruce, **f.** *Pontoniopsis comanthi* Borradaile, **g.** *Stegopontonia commensalis* Nobili, **h.** *Tuleariocaris zanzibarica* Bruce. Scale = 1 mm.

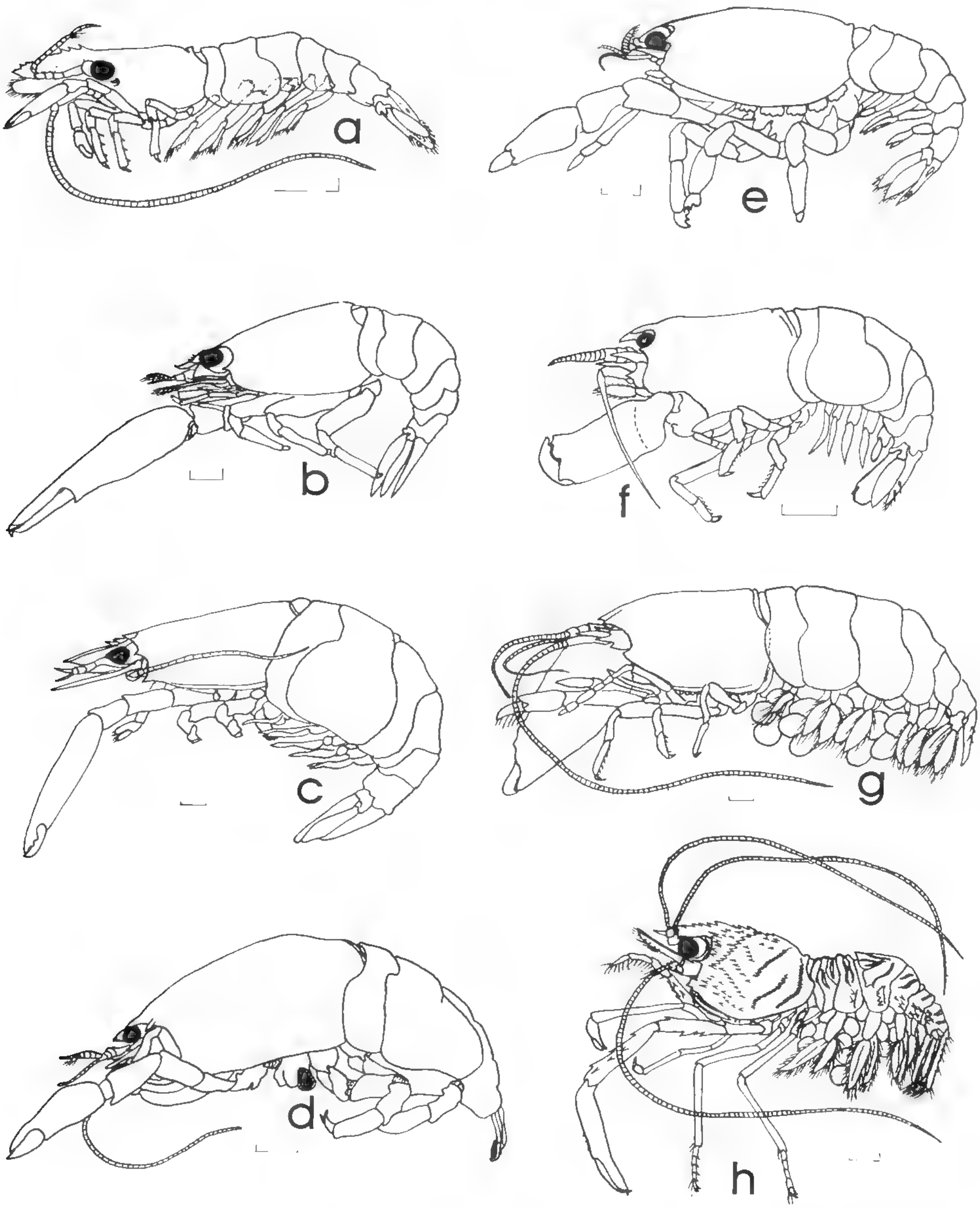

Fig. 2. **a.** *Zenopontonia noverca* (Kemp), **b.** *Levicaris mammillata* (Edmondson) (after Fujino & Takeda, 1977), **c.** *Gnathophylloides robustus* Bruce, **d.** *Pycnocaris chagoae* Bruce, **e.** *Conchodytes meleagrinae*, **f.** *Athanas indicus* (Coutière), **g.** *Synalpheus fossor* (Paulson), **h.** *Odontozona* sp. Scale = 1 mm.

2. First pair of pereiopods slender, second more robust 3
—. Second pair of pereiopods slender, first pair more robust 15
3. Mandible with incisor process; third maxillipeds with ischio-merus slender, not opposing in midline 4
—. Mandible without incisor process; ischio-merus of third maxilliped broadened, operculate 13
4. Mandible with small 2-jointed palp ....*Palaemonella*
—. Mandible without palp 5
5. Rostrum generally dorsally dentate (except in *Periclimenes insolitus* Bruce) 6
—. Rostrum toothless 10
6. Hepatic spine present 7
—. Hepatic spine absent ....*Araiopontonia*
7. Hepatic spine fixed 8
—. Hepatic spine mobile 9
8. Third and fifth pereiopods with hoof-shaped ventral process on dactyl ....*Tuleariocaris*
—. Third and fifth pereiopods without hoof-shaped process on dactyls ....*Periclimenes*
9. First pereiopods with simple chela; protopodite of uropod not with an acute postero-lateral process ....*Allopontonia*
—. First pereiopod with spatulate chela; protopodite of uropod with an acute postero-lateral process ....*Zenopontonia*
10. Second pereiopods subequal and similar 11
—. Second pereiopods unequal and dissimilar 12
11. Hepatic and antennal spines present, epistomal horns present ....*Parapontonia*
—. Hepatic and antennal spines absent, epistomal horns absent ....*Conchodytes*
12. Hepatic spine present ....*Stegopontonia*
—. Hepatic spine absent ....*Pontoniopsis*
13. Second maxilliped with carpus and ischio-meral segments greatly elongated ....*Levicaris*
—. These segments normal 14
14. Rostrum with dorsal teeth present ....*Gnathophylloides*
—. Rostrum without dorsal teeth ....*Pycnocaris*
15. Branchiostegite and pleura greatly broadened, covering pereiopods ....*Pterocaris**

**Pterocaris typica* is an unusual shrimp said to possibly occur on echinoderms (Balss, 1957 p. 1414), although the species is known from only a single specimen from Ambon, Indonesia, and Heller's original account makes no mention of any associations (Heller, 1862). Coutiere (1899) states that the species may possibly be associated with molluscs or echinoderms, but no further evidence is available. The species is included in this key in case it should prove to be associated with echinoderms, as further specimens of this bizarre shrimp would be of great interest.

—. Branchiostegite and pleura normal 16

16. Eyes dorsally covered by carapace; second pereiopods dissimilar and markedly unequal .... *Synalpheus*

—. Eyes dorsally exposed; second pereiopods similar and subequal .... *Athanas*

KEYS TO AND LISTS OF SPECIES OF SHRIMP ASSOCIATED WITH INDO-WEST PACIFIC ECHINODERM HOSTS

Family PALAEMONIDAE

Subfamily PONTONIINAE

Palaemonella Dana

1. *Palaemonella pottsi* (Borradaile, 1915) (fig. 1c)
Distribution: Type locality, Murray Island, Torres Straits.
Also known from Zanzibar, Kenya, Singapore, Japan, New Caledonia, the Great Barrier Reef and Marshall Islands.

Crinoid hosts: *Comanthina schlegeli* (P. H. Carpenter), *Comanthus bennetti* (J. Müller); *C. parvicirrus* (J. Müller); *C. timorensis* (J. Müller).

Periclimenes Costa

A large genus the members of which are associated with sponges, a wide variety of coelenterates and gastropods, with several free-living predatory species.

A KEY TO CRINOID ASSOCIATED *PERICLIMENES* SPECIES

1. Cornea conoidally produced 2

—. Cornea globular 4

2. Ventral rostral margin with teeth** 3

—. Ventral rostral margin without teeth; R $\frac{2\text{-}3^{**}}{0}$ .... *P. ceratophthalmus*

3. Chelae of second pereiopods subequal; long and slender palm 3.0 times longer than wide and subequal to fingers; R $\frac{6}{1}$ .... *P. amboinensis*

—. Chelae of second pereiopods unequal, short and stout, palm 2.5 times longer than wide and double length of fingers; R $\frac{7}{1}$ .... *P. cornutus*

4. Supraorbital spines absent 5

—. Supraorbital spines present, R $\frac{5\text{-}6}{1\text{-}2}$ .... *P. commensalis*

5. Ventral rostral teeth absent 6

—. Ventral rostral teeth present 7

6. Second pereiopods small, subequal, similar; R $\frac{5\text{-}6}{0}$ .... *P. tenuis*

—. Second pereiopods very unequal, dissimilar: R $\frac{3}{0}$ .... *P. attenuatus*

**The number of rostral teeth found in various species is indicated in the following keys by the formula R = number of dorsal rostral teeth over number of ventral rostral teeth.

7. Dactyls of ambulatory pereiopods simple 8

—. Dactyls of ambulatory pereiopods with distinct accessory spines: R $\frac{8}{2}$ .... *P. novaecaledoniae*

8. Propods of ambulatory pereiopods without ventral spines 9

— Propods of ambulatory pereiopods with ventral spines 10

9. Dactyl of major second pereiopod with distinct lateral flange; R $\frac{10}{3}$ .... *P. carinidactylus*

— Dactyl of major second pereiopod without lateral flange; R $\frac{7}{1}$ .... *P. affinis*

10. Major second pereiopod with fingers much less than half palm length, ischium much longer than merus; R $\frac{7\text{-}8}{1\text{-}2}$ .... *P. ruber* sp. nov

— Major second pereiopod with fingers exceeding half palm length, ischium much shorter than merus; R $\frac{6}{1}$ .... *P. brocketti*

2. *Periclimenes amboinensis* (De Man, 1888)

Distribution: Type locality, Ambon, Indonesia. No subsequent records.

Crinoid host: *Comantheria briareus* (Bell) (new record).

3. *Periclimenes affinis* (Zehntner, 1894)

Distribution: Type locality, Ambon, Indonesia. Also reported from New Caledonia.

Crinoid host: *Comatula cratera* H. L. Clark (new record); *Comanthus* sp.

4. *Periclimenes ceratophthalmus* Borradaile, 1915

Distribution: Type locality, Hulule, Male Atoll, Maldive Islands. Also known from Kenya, Seychelle Islands, Indonesia, Great Barrier Reef and Palau Islands.

Crinoid hosts: *Himerometra robustipinna* (P. H. Carpenter); *Dichrometra afra* A. H. Clark; *Lamprometra klunzingeri* (Hartlaub); *Stephanometra indica* (Smith) (new record); *S. spicata* (P. H. Carpenter).

5. *Periclimenes cornutus* Borradaile, 1915

Distribution: Type locality, Hulule, Male Atoll, Maldive Islands. There have been no subsequent records.

Crinoid host: indet.

6. *Periclimenes commensalis* Borradaile, 1915

Distribution: Type locality, Murray Island, Torres Straits. Also known from Mozambique, Zanzibar, Kenya, Indonesia, Great Barrier Reef, New Caledonia and Palau Islands.

Crinoid hosts: *Capillaster multiradiatus* (Linnaeus); *Comanthina belli* (P. H. Carpenter); *Comanthus bennetti* (J. Müller); *C. parvicirrus* (J. Müller); *C. timorensis* (J. Müller); *Comaster distinctus* (P. H. Carpenter); *Comatella nigra* (P. H. Carpenter) (new record); *Zygometra microdiscus* (Bell); *Heterometra africana* (A. H. Clark); *Himerometra robustipinna* (P. H. Carpenter); *Tropiometra afra* (Hartlaub) (new record).

7. *Periclimenes brocketti* Borradaile, 1915

Distribution: Type locality, North Male Atoll, Maldive Islands. There have been no subsequent reports of this species, which may be synonymous with *P. affinis* (Zehntner).

Crinoid host: indet.

8. *Periclimenes novaecaledoniae* Bruce, 1968

Distribution: Type locality, Ilôt Maître, Noumea, New Caledonia. No further records.

Crinoid host: *Tropiometra afra* (Hartlaub).

9. *Periclimenes carinidactylus* Bruce, 1969

Distribution: Type locality, Bottle and Glass Rocks, Port Jackson, Australia. No further records.

Crinoid host: indet.

10. *Periclimenes tenuis* Bruce, 1969 (fig. 8c)

Distribution: Type locality, Chukwani, Zanzibar. Also known from Eylath, Gulf of Aqaba.

Crinoid hosts: *Heterometra africana* (A. H. Clark); *H. savignyi* (J Müller) *Himerometra robustipinna* (P. H. Carpenter) (new record); *Lamprometra klunzingeri* (Hartlaub); *Decametra chadwicki* (A. H. Clark); *Tropiometra carinata* (Lamarack).

11. *Periclimenes attenuatus* Bruce, 1971 (fig. 8g)

Distribution: Type locality, Waterhouse Cove, Burukule, Duke of York Islands. No futher records.

Crinoid host: indet.

12. ***Periclimenes ruber*** sp. nov. (figs. 3-5, 8f)

MATERIAL EXAMINED: Holotype (Australian Museum, P.28106), ovigerous female; 2 paratypes (Australian Museum, P.28107 ♂; Riksmuseum, Leiden, D31955 ♀) ovigerous female and young male, collected by C. T. Liron, Bribie Passage, Pumicestone Channel, Queensland, Australia, in 8 m depth, 23-4-69, from crinoid host: *Zygometra microdiscus* (Bell).

DESCRIPTION: The holotype is a small slenderly built pontoniine shrimp with a post-orbital carapace length of 2.5 mm. The second ovigerous female (paratype) has a post-orbital carapace length of 2.4 mm and the male (paratype) of 1.9 mm.

Rostrum well developed, reaching to end of antennular peduncle, horizontal, with moderately deep lamina. Lateral carina feebly developed, dorsal margin with seven or eight small acute, evenly spaced teeth; ventral margin feebly convex with one or two small distal teeth. Dorsal teeth situated over or slightly posterior to posterior orbital margin. Supraorbital and epigastric teeth absent. Orbit obsolete. Inferior orbital angle produced, sub-acute. Antennal spine slender, marginal, situated close below inferior orbital angle. Hepatic spine well developed, robust, below and well behind antennal spine. Antero-lateral angle of carapace slightly produced, rounded. Third abdominal segment slightly produced in midline posterodorsally; sixth segment about 1.8 times the length of fifth, and about 1.8 times longer than deep. Pleura of first three segments broadly rounded, fourth and fifth bluntly produced. Telson about 1.3 times length of sixth abdominal segment, three times longer than wide,

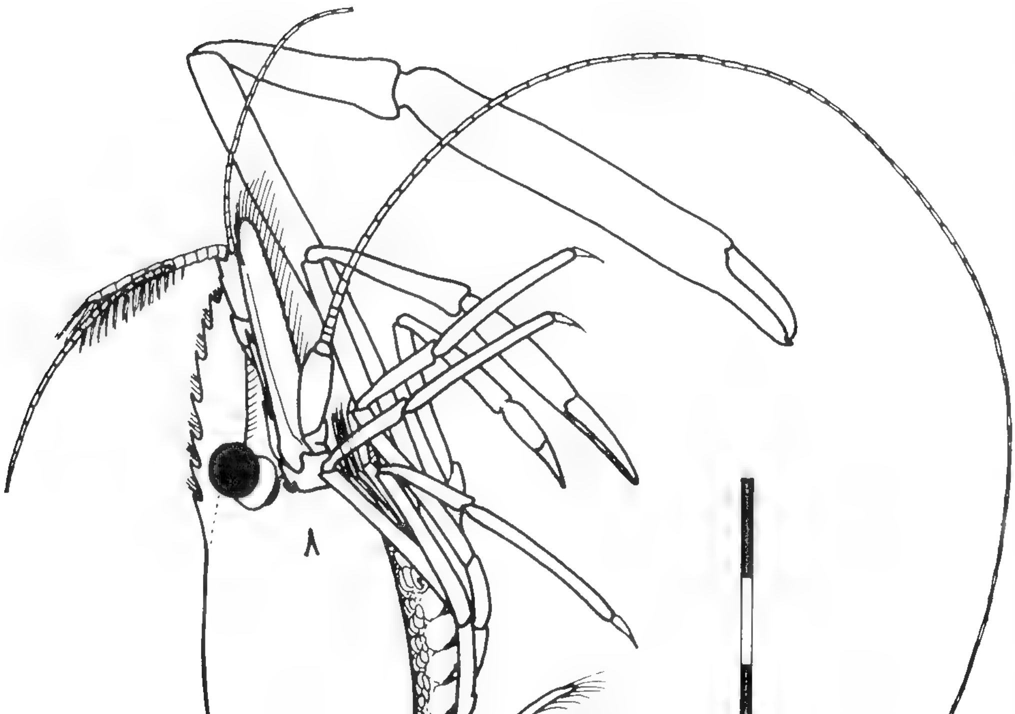

Fig. 3. *Periclimenes ruber* sp. nov., holotype, scale = 1 mm.

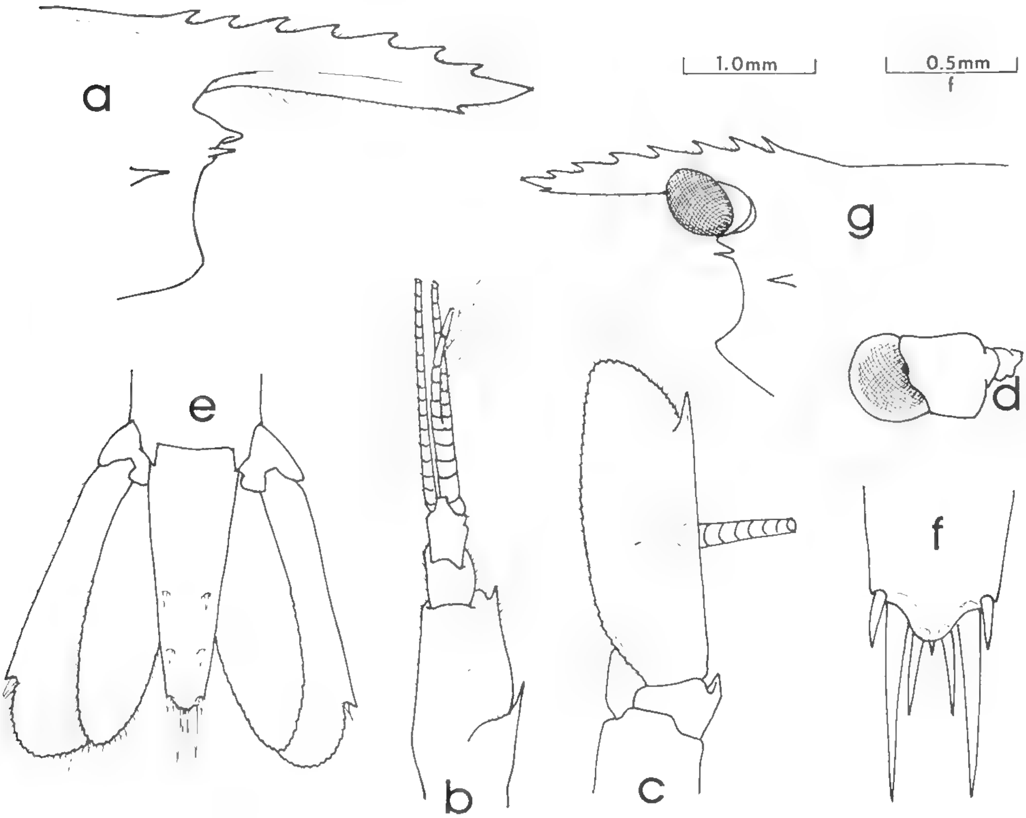

Fig. 4. *Periclimenes ruber* sp. nov., paratype, female. **a.** anterior carapace and rostrum, **b.** antennule, **c.** antenna, **d.** eye, **e.** caudal fan, **f.** posterior telson spines, **g.** paratype, male, anterior carapace and rostrum.

tapering, with rounded posterior margin with small median point. Two pairs of dorsal spines present at 0.6 and 0.8 of telson length. Three pairs of posterior spines present, intermediate spines twice as long as submedian and three times longer than lateral spines.

Proximal segment of antennular peduncle twice as long as broad, produced disto-laterally with a small lobe and slender lateral tooth. Stylocerite slender, reaching middle of segment length. Slender spine present at one third of the ventral medial border. Intermediate and distal segments short, subequal, together equal to half length of proximal segment. Upper flagellum slender, biramous, with proximal 4-5 segments fused; short ramus with five free segments, longer with about 35. Lower flagellum filiform, about 30 segments. Antenna with basicerite with small lateral tooth; carpocerite short and stout, reaching to middle of scaphocerite. Scaphocerite exceeding rostrum and antennular peduncle, three times longer than broad, well developed distal lobe of lamina extending far beyond strong disto-lateral tooth. Flagellum well developed, slender. Eye with short stout peduncle and large globular cornea. Accessory pigment spot present.

First pereiopod moderately slender, fingers equal to half palm length, simple; palm subcylindrical, 2.3 times longer than deep; carpus slightly longer than chela and slightly shorter than merus. Ischium and basis normal, coxa with a distinct slender setose medial ventral process. Second pereiopods well developed, markedly unequal. In female major chela slender and elongated, palm five times longer than wide, smooth, oval in section, three times length of fingers. Fingers robust, small hooked tips, distal cutting edges entire, proximal cutting edges

with one small blunt tooth on dactyl and two on fixed finger. Carpus about half palm length, unarmed. Merus slender, unarmed, about 1.4 times carpus length, 6.5 times longer than wide, and slightly shorter than the slender ischium. Minor chela much smaller and more slender, chela equal to 0.6 of palm length of major chela; fingers slender, slightly shorter than palm, unarmed, with entire cutting edges. Carpus about 1.2 of palm length, and slightly shorter than merus. Ischium about 1.2 of meral length. In male (paratype), major chela is intermediate between major and minor chelae in female, fingers half palm length, unarmed. Ambulatory pereipods slender; dactyls slender, simple with clearly demarkated slender unguis; propod with ventral border spinulate, with distal groups of spines in pairs. Carpus, merus and ischium normal. Pleopods typical for the genus. Uropods exceed tip of telson; lateral border of exopod straight, with very small distal tooth with much larger mobile spine medially.

COLOUR: Uniform dark red over body and appendages, except tips of uropods and telson and a small dorsal spot on the third abdominal segment, which are yellow.

REMARKS: *Periclimenes ruber* is most remarkable for its long slender major second pereiopod, in which the merus far outreaches the distal border of the scaphocerite. It is most closely related to *P. affinis*, which also has markedly unequal second periopods, although to a lesser extent, but has the propods of the ambulatory pereiopods without ventral spines. The only other shrimp known to associated with *Zygometra microdiscus* is *P. commensalis*, which can easily be distinguished from *P. ruber* by the presence of distinct supraorbital spines and short, stout, subequal chelae on the second pereiopods.

A KEY TO THE ASTEROID ASSOCIATED *PERICLIMENES* SPECIES

1. Disto-lateral angle of proximal segment of antennular peduncle with a single tooth only, R .... *P. parasiticus*

— Disto-lateral angle of proximal segment of antennular peduncle with 2-3 teeth, R .... *P. soror*

13. *Periclimenes parasiticus* Borradaile, 1898

Distribution: Type locality, Milne Bay, New Guinea. No subsequent records. Probably juvenile specimens of *P. soror*.

Asteroid host: *Linckia* sp.

14. *Periclimenes soror* Nobili, 1904 (figs. 6b-d, 7a, d, 8e).

Distribution: Type locality, Jibouti. Common throughout the whole Indo-West Pacific region and recently found to occur also in the Gulf of Panama.

Asteroid hosts: *Choriaster granulatus* Lütken; *Culcita novaeguineae* Müller & Tröschel; *C. schmideliana* (Retzius); *Pentaceraster horridus* (Gray); *P. mammillatus* (Audouin); *P. regulus* (Müller & Tröschel). (New record); *P. tuberculatus* (Müller & Tröschel); *P. hawaiiensis* (Fisher); *Protoreaster lincki* (de Blainville); *P. nodosus* (Linnaeus); *Linckia multifora* (Lamarck); *Acanthaster brevispina* Fisher; *A. planci* (Linnaeus); *Mithrodia clavigera* (Lamarck); *M. bradleyi* Verrill; *Echinaster purpureus* (Gray).

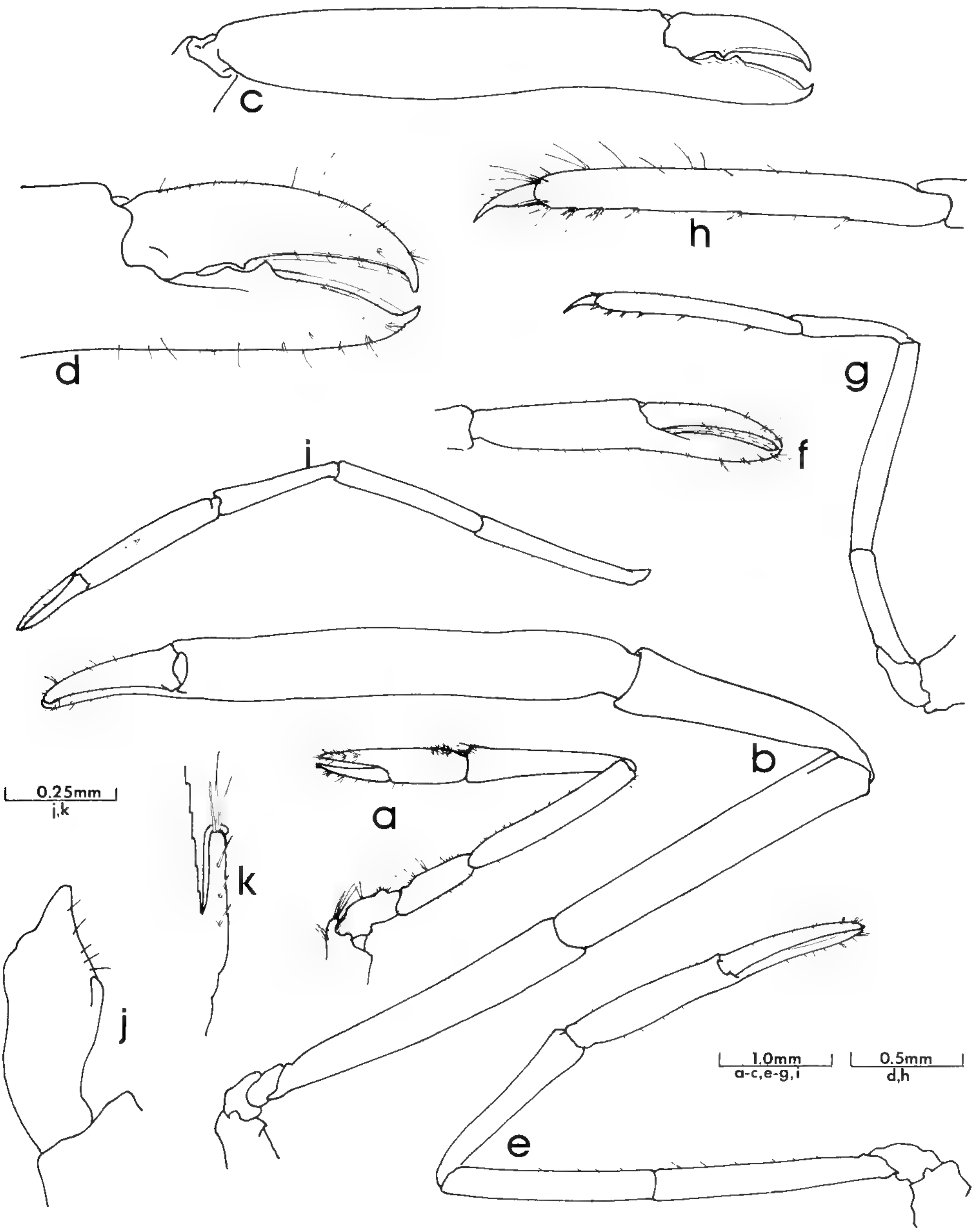

Fig. 5. *Periclimenes ruber* sp. nov., paratype, female. **a.** first pereiopod, **b.** major second pereiopod, **c.** chela of major second pereiopod, **d.** fingers of major second pereiopod, **e.** minor second pereiopod, **f.** chela of minor second pereiopod, **g.** third pereiopod, **h.** propod and dactyl of third pereiopod, **i.** paratype, male, second pereiopod, **j.** endopod of first pleopod, **k.** appendix interna and appendix masculina.

OPHIUROID ASSOCIATED *PERICLIMENES* SPECIES

15. *Periclimenes lanipes* Kemp, 1922

Distribution: Type locality, Mergui Archipelago. Also recorded from Madagascar, Zanzibar, Kenya, Somalia, New Caledonia and Queensland, Australia.

Ophiuroid hosts: *Euryale purpurea* Mortensen; *Astroboa nuda* (Lyman); *Astroglymma sculptum* (Döderlein).

A KEY TO THE ECHINOID ASSOCIATED *PERICLIMENES* SPECIES

1. Supraocular teeth (arising from the well-defined orbital margin) present 2
— Supraocular teeth absent 4
2. Rostrum without teeth, R $\frac{0}{0}$ .... *P. insolitus*
— Rostrum with small distal dorsal teeth only 3
3. Palm of first pereiopods sub-equal to fingers, not compressed; fingers subspatulate, dactyl without dorsal carina, R $\frac{3\text{-}7}{0}$ .... *P. zanzibaricus*
— Palm of first pereiopod short, half length of fingers; fingers feebly subspatulate, dactyl with dorsal carina, R $\frac{5}{0}$ .... *P. cristimanus*
4. Merus of ambulatory pereiopods with disto-ventral tooth................................ 5
— Merus of ambulatory pereiopods unarmed.. 6
5. Dactyls of ambulatory pereiopods without accessory tooth R $\frac{9\text{-}10}{0\text{-}1}$ .... *P. maldivensis*
— Dactyls of ambulatory pereiopods with robust accessory spine, R $\frac{7\text{-}8}{1}$ .... *P. colemani*
6. Generally glabrous; ventral rostral teeth present, R $\frac{6}{2}$ .... *P. hertwigi*
— Generally hirsute; ventral rostral teeth absent, R $\frac{8}{0}$ .... *P. hirsutus*

16. *Periclimenes hertwigi* Balss, 1913

Distribution: Type locality, Sagami Bay, Japan. Also recorded from Indonesia and Queensland, Australia.

Echinoid host: *Araeosoma thetidis* (H. L. Clark); *Phormosoma* sp.

17. *Periclimenes cristimanus* Bruce, 1965

Distribution: Type locality, Singapore. Also recorded from Hong Kong and Heron Island, Queensland.

Echinoid hosts: *Diadema setosum* (Leske); *Echinothrix calamaris* (Pallas) (new record).

18. *Periclimenes maldivensis* Bruce, 1969

Distribution: Type locality, Suvadiva Atoll, Maldive Islands. No subsequent records.

Echinoid host: indet.

19. *Periclimenes zanzibaricus* Bruce, 1969

Distribution: Type locality, Fawatu, Zanzibar. Also recorded from Kenya, the Seychelle Islands and Western Australia.

Echinoid hosts: *Centrostephanus tenuispinus* H. L. Clark; *Diadema savignyi* Michelin; *D. setosum* (Leske); *Echinothrix calamaris* (Pallas).

20. *Periclimenes hirsutus* Bruce, 1971 (fig. 1e).

Distribution: Type locality, Nukulau Is., Suva, Fiji. Also known from Zanzibar and the Seychelle Islands.

Echinoid hosts: *Astropyga radiata* (Leske).

21. *Periclimenes insolitus* Bruce, 1974

Distribution: Type locality, Waikiki, Honolulu, Hawaii. No subsequent records.

Echinoid host: *Pseudoboletia indiana* (Michelin).

22. *Periclimenes colemani* Bruce, 1975

Distribution: Type locality, Heron Island, Queensland, Australia. No further records.

Echinoid host: *Asthenosoma intermedium* H. L. Clark.

A KEY TO THE HOLOTHURIAN ASSOCIATED *PERICLIMENES* SPECIES

1. Rostrum with narrow lamina, less than 20 dorsal teeth, ventral rostral teeth present 2
— Rostrum with wide lamina, more than 20 dorsal teeth, ventral rostral teeth absent 3
2. Posterior rostral teeth mobile; chela of first pereiopod not spatulate, $R\frac{10\text{-}14}{2\text{-}3}$ .... *P. hongkongensis*
— Posterior rostral teeth fixed; chela of first pereiopod spatulate; $R\frac{9}{1}$ .... *P. pectiniferus*
3. Epigastric spine (situated on the dorsal mid-line of the carapace, posterior to the base of the rostrum) present; disto-lateral angle of proximal segment of antennular peduncle unidentate, dactyls of ambulatory pereiopods biunguiculate $R\frac{22}{0}$ .... *P. rex*
— Epigastric spine absent; disto-lateral angle of proximal segment of antennular peduncle multidentate; dactyls of ambulatory pereiopods with accessory spine obsolete, $R\frac{23\text{-}30}{0}$ .... *P. imperator*

23. *Periclimenes rex* Kemp, 1922

Distribution: Type locality, Port Blair, Andaman Islands. Also reported from Madagascar and Moçambique.

Holothuroid hosts: *Thelenota ananas* (Jaeger); *Synapta maculata* (Chamisso & Eysenhardt).

24. *Periclimenes pectiniferus* Holthuis, 1952

Distribution: Type locality, Kabala dua Island, Borneo Bank. Otherwise known only from east of Townsville, Australia.

Holothuroid host: indet.

25. *Periclimenes imperator* Bruce, 1967

Distribution: Type locality, Chumbe Island, Zanzibar. Also recorded from Madagascar, Kenya, Sinai, Seychelle Islands, Comoro Islands, Great Barrier Reef, Palau Islands and Hawaii.

Holothuroid hosts: *Stichopus chloronotus* Brandt; *S. variegatus* Semper; *Bohadschia* sp.; *Thelenota ananas* (Jaeger); *Opheodesoma spectabilis* Fisher; *Synapta maculata* (Chamisso & Eysenhardt).

P. imperator commonly occurs on the nudibranch genus *Hexabranchus*.

26. *Periclimenes hongkongensis* Bruce, 1969

Distribution: Type locality, Rocky Harbour, Hong Kong. No subsequent records.

Holothuroid host: indet.

Allopontonia Bruce

27. *Allopontonia iaini* Bruce, 1972 (fig. 1a)

Distribution: Type locality, Zanzibar Harbour. Also reported from Kenya.

Echinoid host: *Salmaciella dussumieri* (L. Agassiz).

Zenopontonia Bruce

28. *Zenopontonia noverca* (Kemp, 1922) (fig. 2a)

Distribution: Type locality, New Caledonia. Also reported from Zanzibar and Queensland, Australia.

Asteroid hosts: *Culcita novaeguineae* Müller & Tröschel; *C. schmideliana* (Retzius); *Pentaceraster alveolatus* (Perrier); *P. tuberculatus* (Müller & Tröschel); *P. hawaiiensis* (Fisher); *Poraster superbus* (Möbius); *Protoreaster lincki* (de Blainville).

Stegopontonia Nobili, 1906

29. *Stegopontonia commensalis* Nobili, 1906 (figs. 1g, 6a, 8d)

Distribution: Type locality, Hao, Tuamotu Islands. Also recorded from Kenya, Mauritius and Seychelle Islands, New Caledonia, Great Barrier Reef and Hawaii.

Echinoid hosts: *Diadema savignyi:* Michelin; *D. setosum* (Leske); *D. paucispinum* A. Agassiz; *Diadema* sp.: *Echinothrix calamaris* (Pallas); *E. diadema* (Linnaeus).

Tuleariocaris Hipeau-Jacquotte

A KEY TO THE ECHINOID ASSOCIATED *TULEARIOCARIS* SPECIES

1. Highly elongated body form, R $\frac{8\text{-}10}{1\text{-}5}$ ....*T. zanzibarica*

—. More robust body form, R $\frac{6\text{-}8}{0}$ ....*T. holthuisi*

30. *Tuleariocaris holthuisi* Hipeau-Jacquotte, 1965

Distribution: Type locality, Tulear, Madagascar. Also reported from Hawaii and Kenya.

Echinoid hosts: *Astropyga radiata* (Leske); *Echinothrix diadema* (Linnaeus); *Stomopneustes variolaris* (Lamarck); *Echinometra mathaei* (de Blainville).

31. *Tuleariocaris zanzibarica* Bruce, 1967 (figs 1h, 7b, 8a-b)

Distribution: Type locality, Mtoni, Zanzibar. Also reported from Madagascar, Kenya, Japan (?) and Bougainville Island.

Echinoid hosts: *Astropyga radiata* (Leske); *Diadema savigny:* Michelin; *D. setosum* (Leske); *Echinothrix calamaris* (Pallas); *E. diadema* (Linnaeus).

Parapontonia Bruce

32. *Parapontonia nudirostris* Bruce, 1968 (fig. 1d)

Distribution: Type locality, Tiare Bay, New Caledonia. Also reported from Queensland, Australia.

Crinoid hosts: *Himerometra robustipinna* (P. H. Carpenter) (new record); *Tropiometra afra* (Hartlaub).

Araiopontonia Fujino & Miyake

33. *Araiopontonia odontorhyncha* Fujino & Miyake, 1970 (fig. 1b)

Distribution: Type locality, Amami Islands, Japan. There have been no subsequent reports.

Crinoid host: indet.

Pontoniopsis Borradaile, 1915

34. *Pontoniopsis comanthi* Borradaile, 1915 (figs 1f, 8h)

Distribution: Type locality, Mabuaig, Torres Strait. Also reported from Zanzibar, Kenya, Gulf of Aqaba, Indonesia, Gilbert and Marianna Is.

Crinoid hosts: *Comanthus timorensis* (J. Müller); *Comatula pectinata* (Linnaeus) (new record); *C. purpurea* (J. Müller) (new record); *Heterometra savignyi* (J. Müller); *Lamprometra klunzingeri* (Hartlaub); *Tropiometra carinata* (Lamarck).

Conchodytes Peters

35. *Conchodytes tridacnae* Peters, 1852 (fig. 2e)

Distribution: Type locality, Ibo, Mocambique. Also known throughout the Indo-West region, from the Red Sea to Hawaii.

Holothuroid host: indet.

C. tridacnae is usually associated with the bivalve genus *Tridacna*.

Family GNATHOPHYLLIDAE

Gnathophylloides Schmitt

A KEY TO THE ECHINOID ASSOCIATED *GNATHOPHYLLOIDES* SPECIES

1. Rostrum short, scarcely reaching beyond cornea, R $\frac{3\text{-}4}{1}$ .... *G. mineri*
—. Rostrum long and broad, extending far beyond cornea, R $\frac{2\text{-}3}{0}$ .... *G. robustus*

36. *Gnathophylloides mineri* Schmitt, 1933

Distribution: Type locality, Enserioda, Puerto Rico. Also recorded from Zanzibar, Seychelle Islands, Hawaii, Barbados, Florida, Yucatan, Jamaica, Antigua Island, Tobago cays and Bahia de la Ascension.

Echinoid hosts: *Pseudoboletia indiana* (Michelin); *Tripneustes gratilla* (Linnaeus).

37. *Gnathophylloides robustus* Bruce, 1973 (fig. 2c)

Distribution: Type locality, Point Moore, Geraldton, Western Australia. No further records.

Echinoid host: *Centrostephanus tenuispinus* H. L. Clark.

Levicaris Bruce

38. *Levicaris mammillata* (Edmondson, 1931) (figs 2b, 7e)

Distribution: Type locality, Waikiki, Honolulu, Hawaii. Subsequently recorded only from Japan.

Echinoid host: *Heterocentrotus mammillatus* (Linnaeus).

Pycnocaris Bruce

39. *Pycnocaris chagoae* Bruce, 1972 (fig. 2d)

Distribution: Type locality, East Point, Diego Garcia, Chagos Archipelago. No subsequent records.

Holothuroid host: *Holothuria (Semperothuria) cinerascens* (Brandt).

Family ALPHEIDAE

Athanas

A KEY TO THE ECHINOID ASSOCIATED *ATHANAS* SPECIES (ADAPTED FROM SUZUKI, 1970)

1. Well-developed supra-corneal teeth .... *A. borradailei*
—. Without supra-corneal teeth 2
2. With three pairs of epipodites and four pairs of setobranchiae .... *A. acanthocarpus*
—. With two paris of epipodites and three pairs of setobranchiae 3
3. Rostrum proximally broad, triangular in shape. Outer margin of palm of first pereiopod distally angular and sharply pointed at tip .... *A. dorsalis*
—. Rostrum lanceolate 4
4. Outer margin of palm of first pereiopod distally angular, sharply pointed at tip. Pterygostomial margin angular .... *A. indicus*

—. Outer margin of palm of first pereiopod obtusely angular distally. Pterygostomial margin rounded .... *A. kominatoensis*

40. *Athanas dorsalis* (Stimpson, 1861)

Distribution: Type locality, near Hong Kong. Also widespread in Indian Ocean and Western Pacific Ocean, from East Africa east to the Tuamotu Islands.

Echinoid hosts: *Centrostephanus tenuispinus* H. L. Clark; *Echinothrix calamaris* (Pallas) (new record); *E. diadema* (Linnaeus); *Stomopneustes variolaris* (Lamarck); *Tripneustes gratilla* (Linnaeus); *Heliocidaris tuberculata* (Lamarck); *H. erythrogramma* (Valenciennes); *Centrostephanus rodgersi* (A. Agassiz).

41. *Athanas borradailei* (Coutière, 1903)

Distribution: Type locality, Maldive Islands. No subsequent records.

Echinoid host: *Stomopneustes variolaris* (Lamarck).

42. *Athanas indicus* (Coutiere, 1905) (fig. 2f)

Distribution: Type locality not designated. Widespread throughout the Indian Ocean and western Pacific Ocean.

Echinoid hosts: *Diadema* sp.; *Echinometra mathaei* (de Blainville); *Anthocidaris crassispina* (A. Agassiz).

43. *Athanas kominatoensis* Kubo, 1942

Distribution: Type locality, Kominato, Japan. Known only from Japanese waters.

Echinoid host: *Anthocidaris crassispina* (A. Agassiz).

44. *Athanas acanthocarpus* Miya & Miyake, 1968

Distribution: Type locality, Kamiyama-jima, Okinawa Ryu-kyu Islands. Also known from Kenya.

Echinoid host: *Echinometra mathaei* (de Blainville).

Synalpheus Bate, 1888 (fig. 2g)

A KEY TO THE CRINOID ASSOCIATED *SYNALPHEUS* SPECIES (FROM BANNER & BANNER 1975)

1. Dactylus of third leg biunguiculate; without orbito-rostral process 2
—. Dactylus of third leg triunguiculate; with orbito-rostral process .... *S. demani*

2. Disto-inferior margin of merus of third leg with tooth 3
— Disto-inferior margin of merus of third leg inermous..................................... 5
3. Dactylus of small chela crescentic, strongly hooked........................... *S. comatularum*
Dactylus of small chela straight 4
4. Fixed finger of large chela bearing strong flat tooth on medial side....... *S. odontophorus*
— Fixed finger of large chela with medial edge rounded, not projecting......... *S. stimpsoni*

5. Rostral carina strong and continued almost to posterior end of carapace ...... *S. carinatus*

— Rostral carina slight and terminating anterior to eye .... *S. tropidodactylus*

45. *Synalpheus comatularum* (Haswell, 1882)

Distribution: Type locality, Albany Passage, Torres Straits. Numerous records from Australia. Also reported from Ceylon and Singapore.

Crinoid host: *Comanthus timorensis* (J. Müller).

46. *Synalpheus carinatus* (De Man, 1888)

Distribution: Type locality, Ambon, Indonesia. Recorded from Indonesia, Malaysia, Australia and the Caroline, Marshall and Gilbert Islands.

Crinoid hosts: *Comanthina schlegeli* (P. H. Carpenter) (new record); *Comatula purpurea* (J. Müller).

47. *Synalpheus odontophorus* (De Man, 1888)

Distribution: Type localities, Tanahajampeah Island, Kai Islands, and near east coast of Timor. Also known from Sagami Bay, Japan.

Crinoid host: indet.

48. *Synalpheus stimpsoni* (De Man, 1888)

Distribution: Type locality, Ambon, Indonesia. Also known from Singapore, Thailand, Indonesia, Philippines, Japan, Marshall and Gilbert Islands.

Crinoid hosts: *Comanthina schlegeli* (P. H. Carpenter); *Comanthus parvicirrus* (J. Müller); *C. timorensis* (J. Müller); *C. japonicus* (J. Müller); *Comatula purpurea* (J. Müller).

49. *Synalpheus demani* Borradaile, 1900

Distribution: Type locality, Loyalty Islands. Also reported from Red Sea, Indonesia, Philippines, Japan and Marshall Islands.

Crinoid host: *Comanthina schlegeli* (P. H. Carpenter).

50. *Synalpheus tropidodactylus* Banner & Banner, 1975

Distribution: Type locality, off Geraldton, Western Australia. No further records. Association with crinoid is inferred.

Crinoid host: indet.

Family STENOPODIDAE

Odontozona

51. *Odontozona* sp. (fig. 2h)

Specimens of this genus have been found on crinoids off Zanzibar and Ambon, Indonesia.

In the Zanzibar specimens, they closely resemble the host in colour, and were a male and female pair. Another crinoid had a juvenile in association. The Indonesian specimen was also found on a crinoid. A report on these specimens is in preparation.

DISCUSSION

In a study of marine shrimps at Malindi, Kenya, (Bruce, 1976) of the 67 species collected, 57 were known to be 'associates'. Of these, 43.5% were associated with coelenterates, 30% with scleractinian corals, and 6% with echinoderms. A similar study of the pontoniine fauna of the Seychelle Islands (Bruce, 1976) showed 62% were associated with coelenterates and 11% with echinoderms. Although the greatest number of associations at present identified are with coelenterates, a significant proportion are with echinoderms, which rank second in importance above all other phyla as hosts.

The first pontoniine shrimp recorded as an echinoderm associate was *Periclimenes amboinensis* de Man, 1888, found on a crinoid. Subsequently *P. affinis* was reported by Zehntner (1894) from an "*Actinometra*" and Borradaile (1898) reported *P. parasiticus* (which has not been found since) on a black *Linckia*. Nobili (1904) described *P. soror*, a widespread associate of asteroids. Balss, in 1913, reported the first occurrence of a species from deeper water, *P. hertwigi* on an echinoid, *Phormosoma* sp., from 120 m. Borradaile (1915) reported on six species of pontoniine shrimps that had been found in association with crinoids from Torres Straits (*Periclimenes brocketti, P. ceratophthalmus, P. cornutus, P. commensalis, Pontoniopsis comanthi* and *Palaemonella pottsi*). The biology of several of these species was also described by Potts (1915), together with the alpheid shrimps *Synalpheus comatularum* and *S. stimpsoni*. The early collectors frequently did not identify the hosts in any detail and, as some of the shrimps seem to be naturally uncommon, the identities of some of the hosts are still not known with certainty, e.g. *Periclimenes brocketti* Borradaile. Several shrimp species are still very poorly known, and have not been certainly identified since their original descriptions.

At present about 50 species of shrimp are know to associate with echinoderms in the Indo-West Pacific region. Of these, 34 belong to the Pontoniinae and 11 to the Alpheidae. No hippolytid shrimps are known to associate with echinoderms in this region. The small family of Gnathophyllidae contains four species considered as commensals of echinoderms, and it is possible that all species of this family are associated with echinoderms, either as commensals, or as predators, such as *Hymenocera picta* Dana, *Phyllognathia ceratophthalma* (Balss) and presumably *Phyllognathia simplex* Fujino. The only other shrimp associated with echinoderms is a stenopid, *Odontozona* sp., found on crinoids.

The shrimps of the Pontoniinae are found in association with all classes of the echinodermata, although they are most numerous in association with the Crinoidea and Echinoidea. The Alpheid shrimps are associated only with echinoids and crinoids and the commensal gnathophyllid shrimps are associated with echinoids and holothurians only. With the exception of the genus *Periclimenes*, all the other shrimp genera are associated with only a single class of host. The genus *Periclimenes* at present includes 11 species associated with crinoids, 7 with echinoids, 2 (? 1 only) associated with asteroids, 2 with holothurians and one with ophiuroids. Of the 7 other pontoniine shrimp genera, 3 are associated with crinoids, 7 with echinoids, 1 with holothurians and 1 with asteroids.

Very little is known about the life of the shrimps associated with echinoderms, or how they affect their host, if they do at all. In several species the normal shrimp population of a host consists of a single male-female pair. Pairs of more than one genus or even several genera, may be present upon a single host. Much depends upon the size of the host animal, larger hosts being found to harbour more associates than the smaller. *Periclimenes imperator* is almost invariably

found in pairs on holothurians, as are the species of *Synalpheus* found in crinoids. This situation probably applies to most of the smaller hosts, but may also depend to a certain extent on the size of the the shrimp commensals. Thus a crinoid, such as *Comanthus timorensis* which may accommodate only a pair of the larger *Palaemonella pottsi* or *Parapontonia nudirostris*, may well also shelter four or five of the smaller *Periclimenes commensalis*. However, the small crinoid associate *Pontoniopsis comanthi* seems only to occur in pairs. Where only a single adult specimen is found on a host, it probably means that the partner was lost in the course of collection. Larger hosts, such as the nocturnal basket stars, often hold a considerable shrimp population — one example of *Astroboa nuda* was host for 56 specimens of *Periclimenes lanipes*. The smallest specimens in these cases are usually post-larval juveniles that have recently settled after their planktonic larval phase. In most shrimp populations the adult females seem to be almost always ovigerous. The ovary is often clearly visible in some of the more transparent species and is usually packed with large ova when the previous batch of eggs is about to hatch. Hatching of the eggs is followed the same night by moulting and the laying of a further batch of ova, so that the females are only very briefly without external eggs. As far as is known at present, all the shrimps have planktonic larvae. The larvae are distributed by the water currents and thus enabled to colonize further hosts. The duration of planktonic life is unknown and wastage of larvae is probably high. Survival will also depend upon locating an appropriate host animal on which to settle. It is probable that once the post-larval shrimps have settled on an appropriate host, they do not voluntarily leave it. The length of life of the adult shrimps remains quite unknown.

Usually each shrimp genus has its own particular niche on the body of the host, as well as its preferred host. *Athanas* species are usually on the oral surface of the test of their host echinoids, if not on the substrate. *Synalpheus* species sit together on the dorsal surface of the disc of their crinoid hosts. Species of *Tuleariocaris* and *Stegopontonia* cling to the spines of their hosts, where *Periclimenes* species are on the aboral surface of the test. *Periclimenes colemani* pairs occupy a bare area on the surface of their host's test, but how these are made is unknown. With many species their favoured station on the host is also unknown, especially in those species that are so cryptically coloured that they are virtually indiscernable when on their host. In some of these the colour pattern does provide a clue. For instance the tips of the caudal fan in *Pontoniopsis comanthi* and *Periclimenes commensalis* may have conspicuous colour spots that exactly match the tips of the crinoid hosts pinnules, suggesting that their niche is on the host's arm, and possibly on a pinnule with the shrimp's head towards the arm.

Virtually nothing is known about the food materials utilized by the shrimps that feed *in situ* on the host, rather than on the substrate. Stomach contents examined have shown no identifiable material. The mouth-parts of the shrimps show a considerable range of variation, upon which much of their taxonomy, at generic level, is based. This suggests some specialization in feeding or the food materials utilized. In the Pontoniinae, all the echinoderm associates retain well developed exopods on the three pairs of maxillipeds. This contrasts with several of the genera associated with coelenterates in which the exopods of the second and third maxillipeds are lost. In most species the exopods are only moderately developed, for example *Periclimenes soror* (fig. 7a,d), *P. commensalis*, but in others, e.g. *Stegopontonia* (fig. 6a) and *Tuleariocaris* (fig. 7b), they are strongly developed and resemble those of the pontoniine *Coralliocaris* (fig. 7c). In the latter genus they are capable of beating rapidly and forming a vertical current converging on the oral region. Such a current may enable these genera to feed on planktonic organisms. Their normal situation on the spines of *Diadema* or *Echinothrix* would ensure that they were in a position to utilize the passing currents. One of the most remarkable specializations found is in *Levicaris mammillata*, which occurs on *Heterocentrotus mammillatus*. In this species the second maxilliped (fig. 7e), usually a most conservative appendage in carideans, has the carpus and merus greatly elongated. The appearance of the modified appendage strongly suggests that the pair are used for scraping the host's spines and drawing foodstuffs towards the shrimp's mouth.

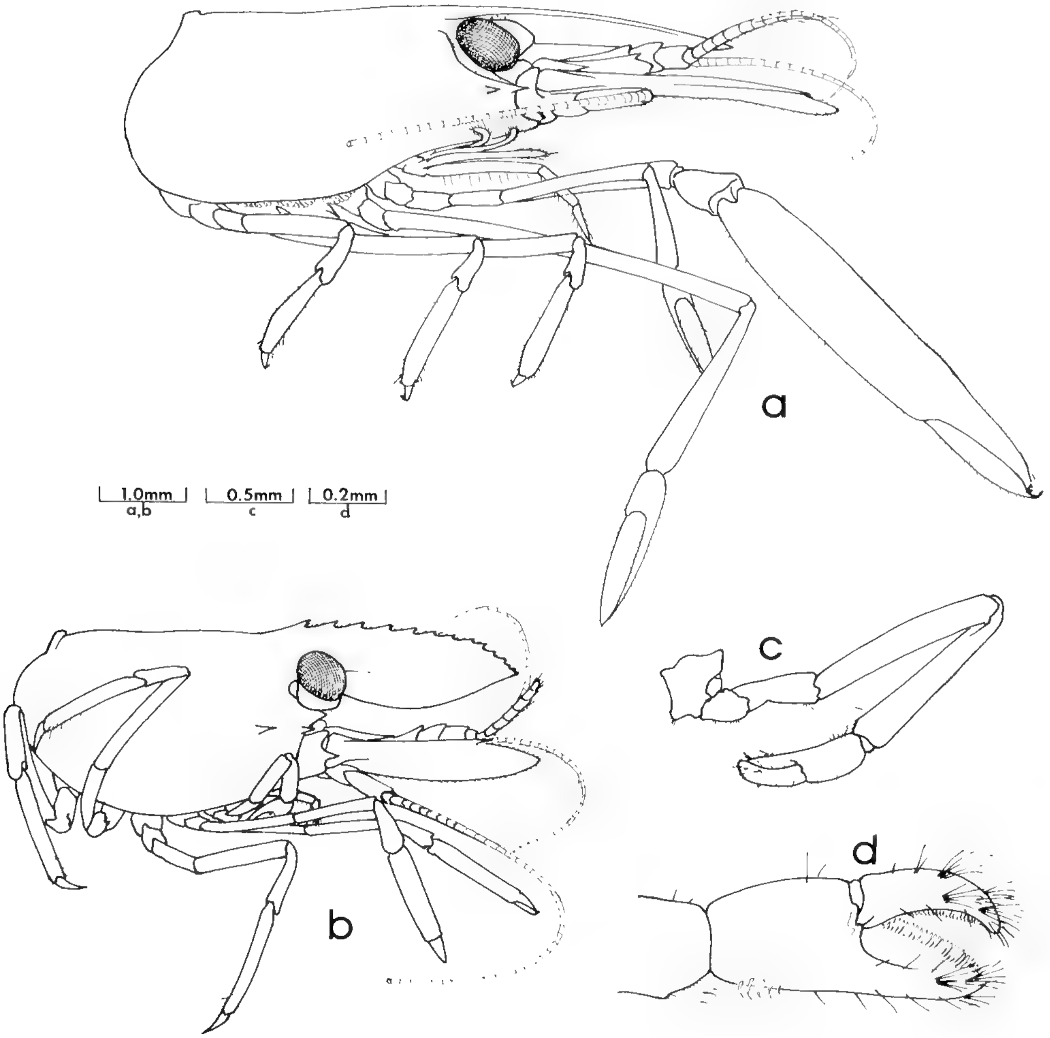

Fig. 6. **a.** *Stegopontonia commensalis* Nobili, cephalothorax and appendages, **b.** *Periclimenes soror* Nobili, cephalothorax and appendages, **c.** *idem,* first pereiopod, **d,** *idem,* chela of first pereiopod.

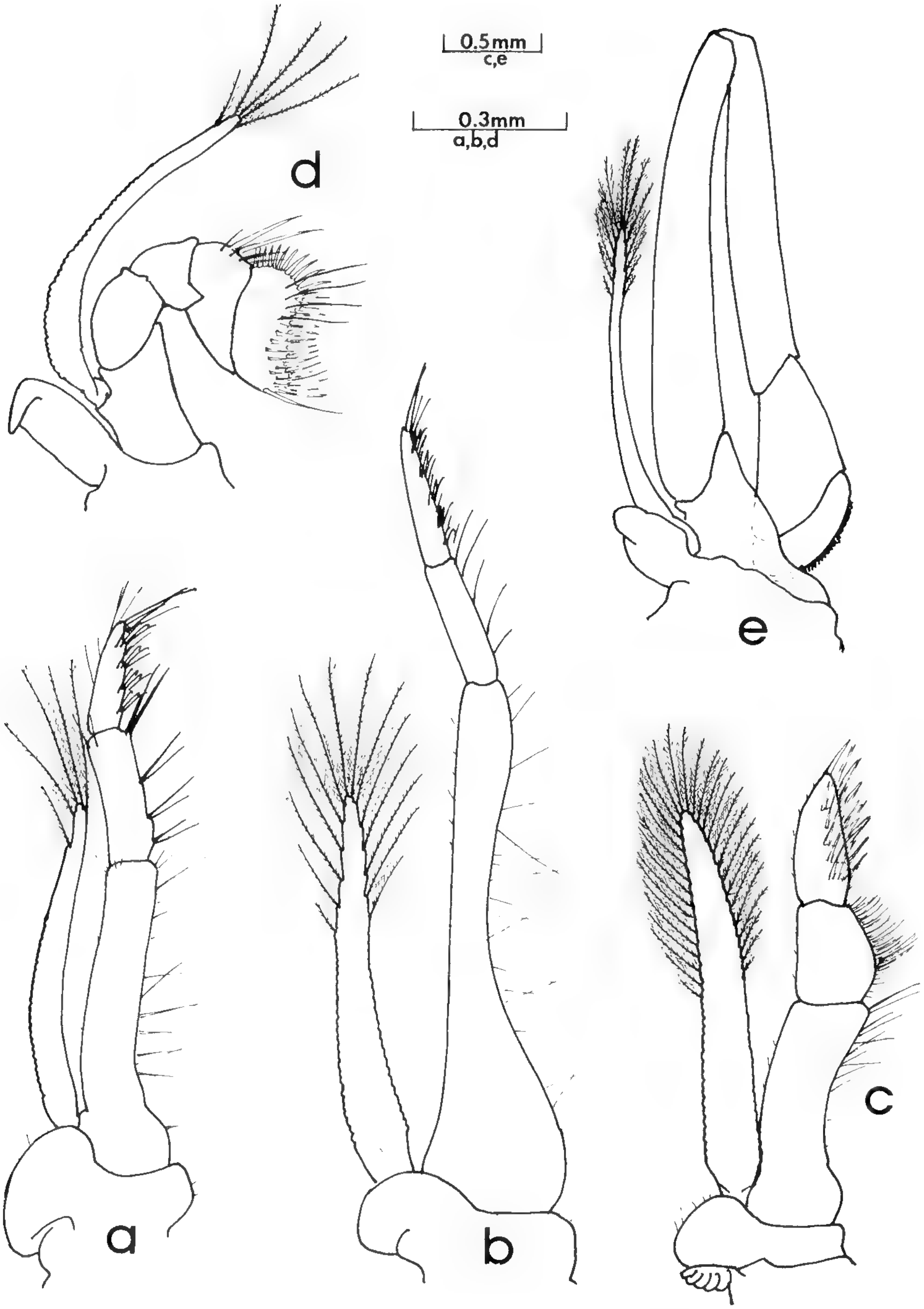

Fig. 7. Third maxillipeds. **a.** *Periclimenes soror* Nobili, **b.** *Tuleariocaris zanzibarica* Bruce, **c.** *Coralliocaris viridis* Bruce; Second maxillipeds, **d.** *Periclimenes soror* Nobili, **e.** *Levicaris mammillata* (Edmondson).

In some species of pontoniine shrimps, such as *Tulcariocaris* spp. the incisor process is greatly reduced. This suggests a diet of soft material in which no cutting up is required. In all the gnathophyllid shrimps, both commensal and free-living, which are closely related to the pontoniines, the incisor produced is completely lacking. Several of the commensal gnathophyllid shrimps have broad opercular ischio-meral segments in the third maxillipeds. Similar maxillipeds also occur in the free-living predatory *Gnathophyllum americanum*, which has been observed using these outer maxillipeds to browse on the extended papulae on the dorsal surface of asteroids. These opercular maxillipeds may have a similar browsing function in the "commensal" species of gnathophyllid shrimps. The first pair of pereiopods are an essential part of the feeding mechanism in pontoniine and gnathophyllid shrimps. In several of the echinoderm associated species the chelae of these appendages have strongly subspatulate fingers (*Periclimenes imperator*, *P. lanipes*) and in some (*P. soror*, *P. pectiniferus*) the cutting edges of these fingers are distinctly denticulate (fig. 6c-d). The reduced incisor process of the mandible and the spatulate chelae of the first pereiopods may be related to a diet of mucus, or mucus and entrapped particles, which may well also form the basis of a common theme running through a wide spectum of commensal associations.

Further evidence of close adaptation of these shrimps to their hosts is shown by the dactyls of the ambulatory pereiopods, with which they cling to the host's surface (fig. 8). These present a wide range of variations, from simple unornamented forms such as *Palaemonella pottsi*, or *Periclimenes ruber* (fig. 8f) to those with distal accessory spines, *P. soror* (fig. 8e) and *Pontoniopsis comanthi* (fig. 8h), or more elaborate forms, *Stegopontonia commensalis* (fig. 8d) or *Tuleariocaris zanzibarica* (fig. 8b) which has a hoof-like ventral process on the third and fifth pereiopods (fig. 8a).

Details have been provided of the range of echinoderms at present known to act as hosts for Indo-West Pacific shrimps. At present 71 host species have been recognised, but undoubtedly many more remain to be identified. Crinoids and echinoids are particularly well represented, and are hosts for a wide variety of shrimps. The asteroids are hosts for only a few pontoniine shrimps and a few holothurians are utilized by a few pontoniine or gnathophyllid shrimps. Ophiuroids are particularly poorly represented as hosts and only the basket stars have attracted a single species of shrimp commensal, *Periclimenes lanipes*. Part of the explanation of this paucity of association lies in the lack of cover offered by the host. Crinoids and echinoids offer well concealed niches that are not provided by most holothurians and many asteroids. Probably also the ventral surface of these mobile animals is too closely in contact with the substrate to provide a suitable living space for animals as large as shrimps. However, some of these can be quite small, being adult at 1 cm total length, and other factors must also be involved. This is also supported by the lack of shrimp commensals on a variety of echinoids and crinoids that would appear to be suitable as hosts. As yet no shrimps have been found in association with cidarid urchins or with stalked crinoids. Most ophiuroids are probably too small and without sufficient ornamentation ot provide a safe niche for commensals.

Where commensal shrimps do live in an exposed situation they usually show the closest resemblance in colour pattern to their host. A good example is *Pycnocaris chagoae* on the holothurian *H. cinerascens*, and also *Periclimenes soror* on *Acanthaster*, in its red and white colour form. In many species the shrimp colour pattern and range of variation is not well known. In several, such as *Gnathophylloides mineri* on *Tripneustes* spp., it may be consistent throughout the whole range of distribution from Kenya to Hawaii and also the Caribbean region. Other species, such as *Periclimenes commensalis*, show a wide range of variations in colouration, each appropriate to its wide range of host species. Some species show two colour forms. *Periclimenes soror* when found on *Culcita*, *Protoreaster* or *Pentaceraster* is usually a deep purple red. When found on *Acanthaster* it is usually a bright red with a conspicuous white dorsal stripe, clearly of

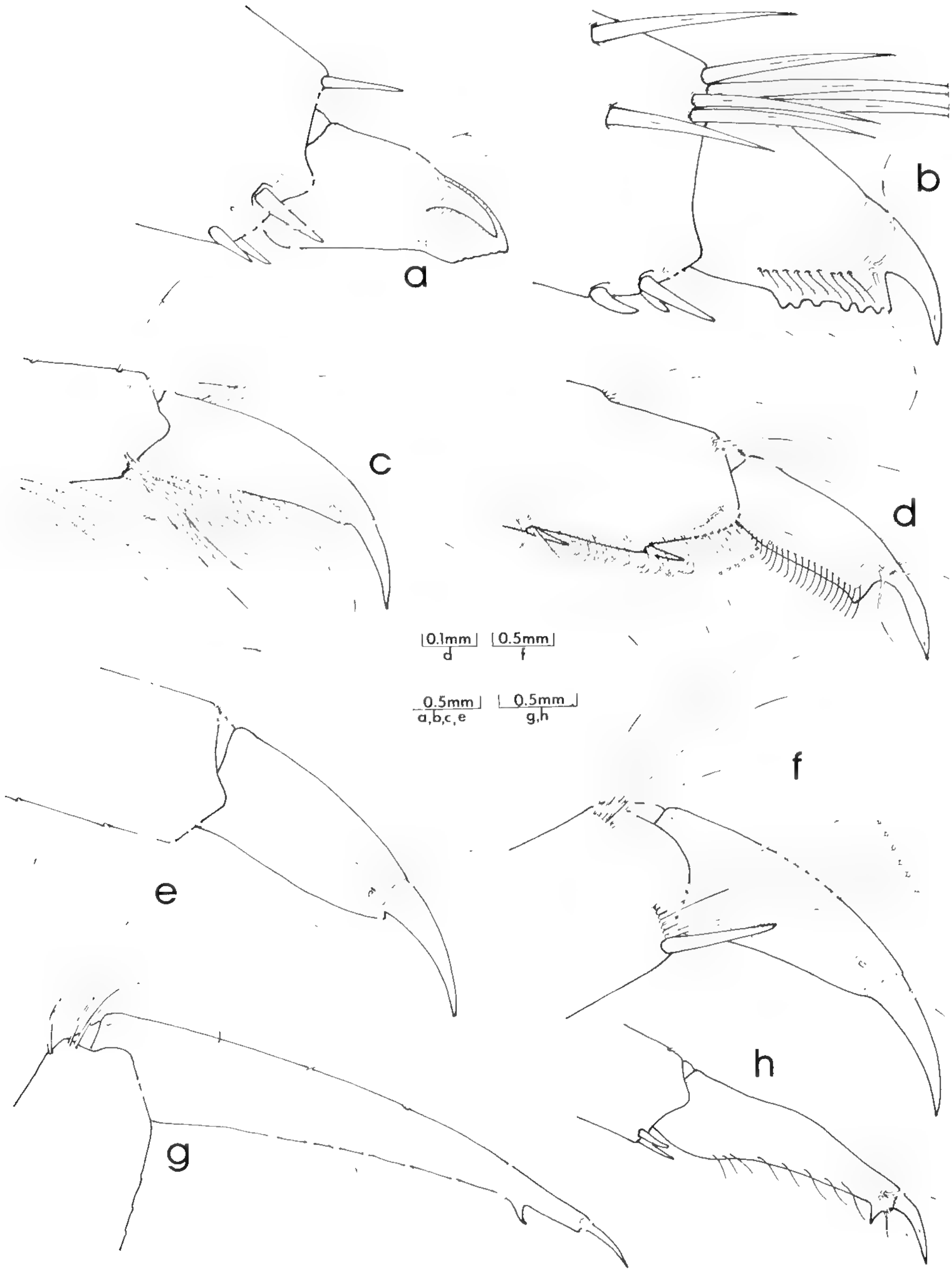

Fig. 8. Dactyls of ambulatory pereiopods. **a.** *Tuleariocaris zanzibarica* Bruce, third pereiopod, **b.** idem, fourth pereiopod, **c.** *Periclimenes tenuis* Bruce, third pereiopod, **d.** *Stegopontonia commensalis* Nobili, third pereiopod, **e.** *Periclimenes soror* Nobili, third pereiopod, **f.** *Periclimenes ruber* sp. nov., third pereiopod, **g.** *Periclimenes attenuatus* Bruce, third pereiopod, **h.** *Pontoniopsis comanthi* Borradaile, third pereiopod.

cryptic value on that host. Occasionally specimens of a particular pattern are found on the "wrong" host, and it may be that this species actually consists of two closely related species that do not show any discernable morphological differences when preserved. In contrast, *Periclimenes imperator*, also with a striking red and white colour pattern, that is very constant throughout its range form the Red Sea to Hawaii, often contrasts conspicuously with its dull coloured holothurian hosts, *Stichopus* and *Bohadschia* spp. The colour pattern is apparently genetically fixed and appropriate to that of the normal host, the red and white nudibranchs of the genus *Hexabranchus*, on which the shrimps are most inconspicuous. This species is one of the few known examples of a shrimp that lives in association with hosts of two different phyla. On the nudibranchs the shrimps nestle amongst the host's gills and are quite difficult to see. Most of the shrimps found on *Diadema* or *Echinothrix* are a dark blue-black colour, often with a fine longitudinal white line. *Athanas indicus* from *Echinothrix* is almost a uniform black colour. *Periclimenes colemani*, found in *Asthenosoma intermedium*, also closely matches its hosts colour pattern, being white with large red spots. In deeper water, *Periclimenes hertwigi* is red, with white tips to the chelae of the second pereiopods and the telson. All show a clear resemblance to their host animals. Some of the species found on crinoids also enhance their cyrptic colour patterns by having large parts of their bodies completely transparent. The dorsal and ventral surfaces of the body are pigmented, so that the shrimp is distinctly visible when viewed from above, but the tissues between are transparent, so that the shrimp is much less easily seen when viewed laterally. This form of colouration is found in *Palaemonella pottsi*, *Periclimenes commensalis* and *P. tenuis*.

Most of the associations mentioned above are from the shallow waters. *Periclimenes hertwigi*, found on *Phormosoma* and *Asthenosoma* in depths of up to 300 m, is the only example known to occur in deeper water as yet. However, a number of pontoniine shrimps are known to occur in deeper water, and some of these species may be associated with echinoderms. *Periclimenes curvirostris* Kubo, from 310 m off Japan, seems to be a particularly likely example, in view of its close resemblance to *P. lanipes*.

One of the strangest associations concerns the pontoniine shrimp *Conchodytes tridacnae*, which has been found in the cloaca of holothurians (Chopra, 1935). This shrimp is normally found in the branchial cavities of giant clams of the genus *Tridacna*. It is another of the rare cases of a commensal being found in association with hosts of different phyla.

Undoubtedly many more shrimp-echinoderm associations remain to be identified and much more needs to be known about the "commensal" relationships involved. The frequency of these associations on coral reefs and in tropical waters generally is one important component in making a major contribution to the high species diversity of these regions. Careful collections by scuba divers can provide the most useful information of these associations in shallow waters as the catches in grab, dredge or trawl hauls are usually inextricably mixed up so that the links between host and commensal are obliterated. Photography from submersibles has not shown much evidence of commensal shrimps in deeper water, but identification of cryptic species under these circumstances on their host is generally impossible. Precise collections from submersibles may provide more information.

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